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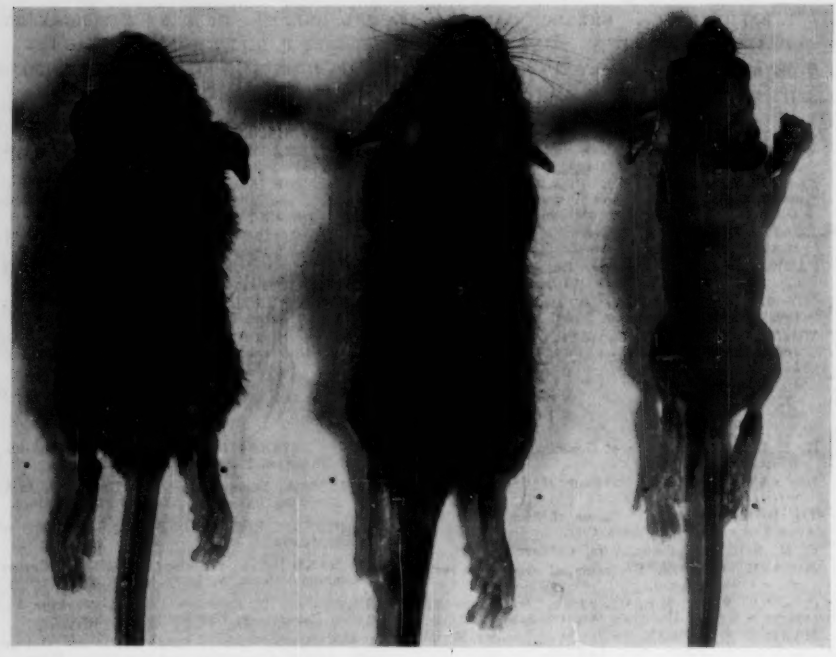

CRINKLED-FUZZY MICE

(SEE PAGE 8)

Lysenko At Bay

Drosophila DDT-Resistance

Descent of Polydactylous Mice

Supernumerary Fragment Chromosomes

VOLUME 49 JANUARY-FEBRUARY, 1958 NUMBER 1

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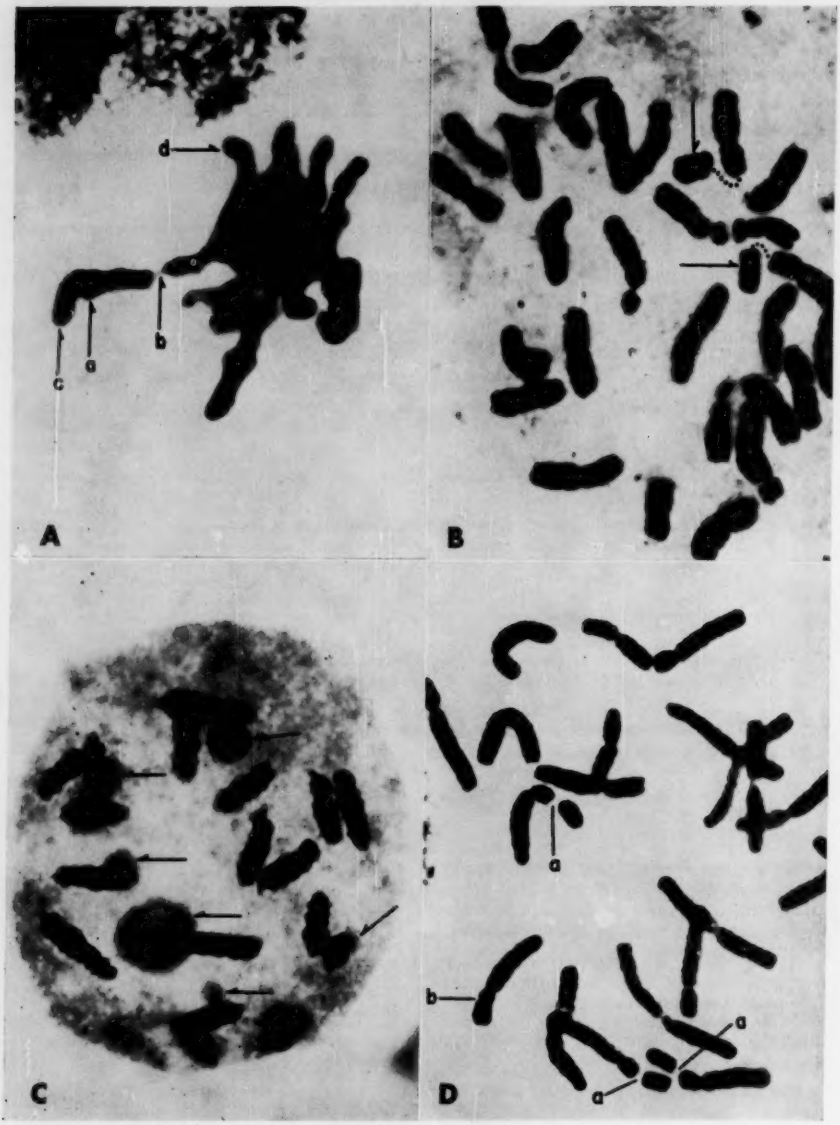


SATELLITE DIFFERENCES BETWEEN PLANTS

Figure 1

A—P.M.C.'s of diploid *Alopecurus pratensis,* satellite pair held together by chiasma (a) with one satellite still attached (b) and the other (c) detached from point (d). *B*—Diploid *A. pratensis* root-tip C-mitotic metaphase with detached satellites (arrows) and parent chromosomes. *C*—P.M.C.'s of haploid *A. pratensis* with six nucleoli (arrows). *D*—*Anthoxanthum odoratum* root-tip C-mitotic metaphase with disarticulating secondary constrictions (points a), and non-disarticulating secondary construction (point b).

A POSSIBLE ORIGIN OF SUPERNUMERARY FRAGMENT CHROMOSOMES

D. MARKARIAN AND J. SCHULZ-SCHAEFFER*

DARLINGTON and Upcott[1] state: "In plants there is a vaguely defined group of chromosomes known by the term supernumerary fragment." This statement points to the fact that probably no other cytological phenomenon confronting the cytologist has proved more difficult to study and understand.

Aside from the cytogenetic status of these fragments, there is a certain vagueness surrounding even the question of nomenclature. The terms supernumerary, fragment, B, and accessory, have been used alone, in combination, and interchangeably to describe the phenomenon. In studies involving mutagens and in other studies where dicentric bridges are formed, the term fragment is used to describe a different phenomenon. The term B is duplicated where the chromosomes are identified alphabetically. In recent studies[9], the term standard fragment has appeared as a consequence of need for a more clearly understood situation.

For the present, no particular confusion arises through this irregularity in nomenclature. However, continued research and understanding of origin, cytology, and genetic importance will no doubt bring about a more exact nomenclature.

The many well-substantiated reports leave no doubt as to the existence of supernumerary fragments. However, during recent root-tip chromosome studies in the genus *Bromus*[13] four species were found to have chromosomes with secondary and tertiary constrictions which disarticulated often during cytological manipulation. The chromosome segments so produced could at first have been interpreted as supernumerary fragments.

Continued observation revealed that these apparent supernumerary fragments were in fact tandem satellites separated from the parent chromosomes through chemical treatment and squashing. This observation led to the speculation that this condition of artifact may be a contributing factor in studies involving supernumerary fragment chromosomes. The present paper concerns an investigation of this possibility.

Materials and Methods

The species investigated were as follows: *Anthoxanthum odoratum* from a natural population in western Washington; *Secale montanum* from a natural population at Pullman, Washington; and *Alopecurus pratensis* from selection P-5903, USDA Plant Material Center, Pullman, Washington.

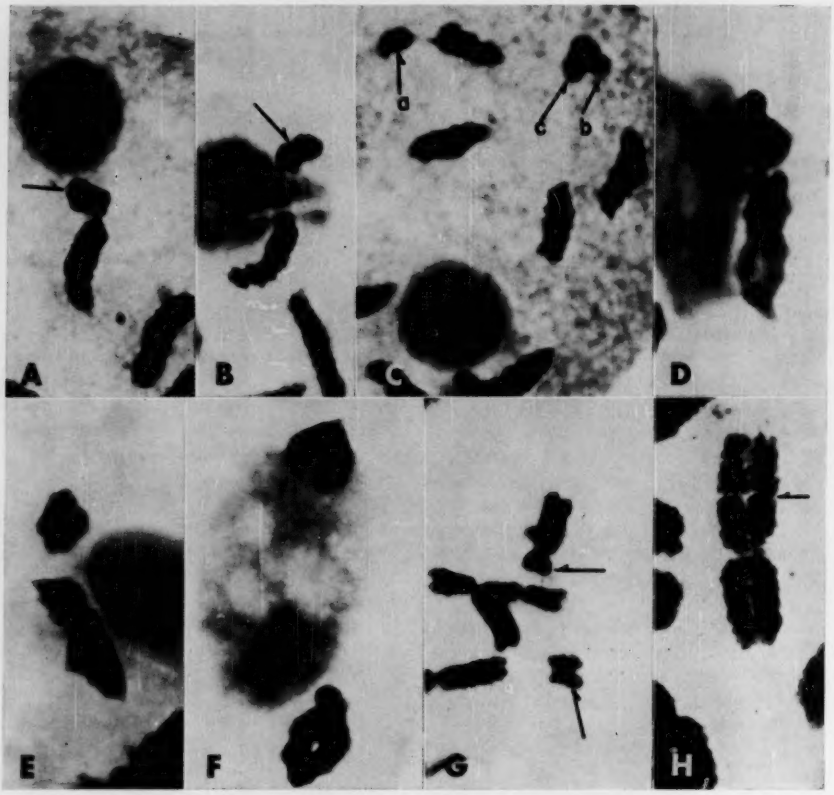
Root-tips were taken from potted plants in the greenhouse. All were treated according to the oxyquinoline technique[10]. Pollen-mother-cells of *A. pratensis* were fixed in three parts alcohol and one part acetic acid and stained with aceto-carmine.

Idiograms were established through measurement of root-tip chromosomes with an eyepiece micrometer. One unit of the scale (Figure 3) equals .55 μ. The measurements represent averages from a minimum of 10 cells in each case.

I. *Alopecurus pratensis*

Rancken[12], Johnsson[5], and Wöhrmann[18] report fragment chromosomes in *A. pratensis*. All three reports agree that a higher percentage of multivalents is found in plants possessing the fragments than in those without. Johnsson

*Assistant Professor, Agronomy Department, State College of Washington and Assistant Professor of Agronomy, Montana State College respectively. Scientific paper No. 1664, Washington Agricultural Experiment Stations. Work conducted jointly under Project No. 1288, State College of Washington and research grant from the German Research Association.



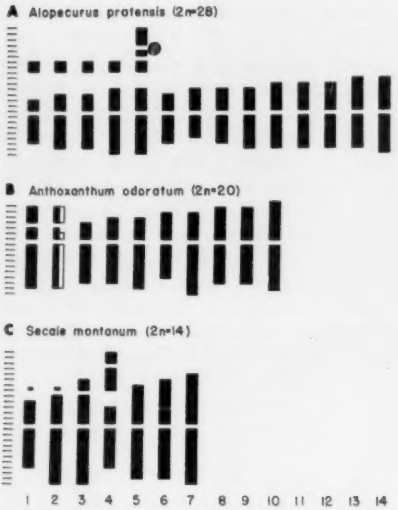
VARIOUS STAGES OF CHROMOSOME DISARTICULATION

Figure 2

A-C—P.M.C.'s of haploid *A. pratensis*. *A* and *B*—Univalent satellites (arrows) associated with parent chromosome 5 (Figure 3 *A*). *C*—Cell with two detached satellites: one (c) from chromosome 5 with attached nucleolus (b), the other (a) less frequently observed. *D-F*—P. M. C.'s of diploid *A. pratensis*. *D*—Satellites attached (chromosome 5). *E* and *F*—Satellites detached. *G* and *H*—Root-tip C-mitotic chromosomes of *S. montanum*. *G*—Chromosome 4 (Figure 3 *C*) and detached satellite (arrows). *H*—Satellite not detached.

also found a higher percentage of bridges and suggests fragments arising from the formation of dicentric chromatid bridges may be the source of the supernumerary fragments. The fact that he never observed the supernumerary fragment paired with a normal chromosome does not support this idea. Johnson observed plants with 1, 2, and 3 supernumerary fragments and Wöhrmann found as many as four.

The mitotic study of root-tips revealed definite differences between plants. Three plants always possessed two supernumerary fragments in each cell observed (Figure 1*B*) while three other plants did not show these fragments. The idiogram in Figure 3*A* shows the morphology of the *A. pratensis* chromosomes determined from this root-tip study. Five pairs of satellited chromosomes are present in this species. Four of the satellite pairs were similar and were easily distinguished from the fifth



IDIOGRAMS OF THE THREE SPECIES
Figure 3

Idiograms were established through measurement of root-tip chromosomes with an eyepiece micrometer. Scale units at left represent 0.55 micron.

pair (chromosome 5, Figure 3*A*). The supernumerary fragments mentioned above were interpreted as satellites detached from chromosome 5 (Figures 1*B* and 3*A*).

Additional evidence for the connection of the supernumerary fragment with chromosome 5 was obtained through meiotic study. One *A. pratensis* plant possessed anthers with haploid P.M.C.'s in addition to anthers with diploid P.M.C.'s. Both types of anthers were found on the same spike.

One disarticulated satellite was found in most of the P.M.C.'s of haploid tissues (Figure 2*A* and 2*B*) and a pair in the diploid (Figure 2*D*, *E* and *F*.) Occasionally there were two fragments in the haploid P.M.C.'s (Figure 2*C* arrows a and c) indicating that at least two pairs could be present in diploid cells. The best evidence for the true nature of the fragment is shown in Figure 2*D* where the satellited bivalent is seen closely associated with the main nucleolus, and the satellite is not detached. Figure 2*A*, *B*, *E* and *F* also show satellite and chromosome close to the nucleolus, indicating that the original position as shown in Figure 2*D* has been changed by artifact.

In his study of meiosis, Wöhrmann[18] (Figure 12) also observed the association of a normal bivalent with one of two supernumerary fragments present, the other lying detached. However, no nucleolus association was noted.

In nearly all of the haploid P.M.C.'s the detached tandem satellite was associated with a small nucleolus as shown in Figures 2*C*, arrow b, and 3*A*. Consequently the five satellited chromosomes have a total of six nucleolar organizer regions instead of the five expected ones. Figure 1*C* illustrates an unusual haploid P.M.C. with six nucleoli in one cell. It is assumed that in late prophase the nucleoli fuse, since only the one large nucleolus associated with chromosome 5 was noted in most cells. The phenomenon of fusion was also observed by Stewart and Bamford[14] in *Medeola virginiana*.

The meiotic metaphase and anaphase behavior of the "fragment" pair never offered evidence of independent centromere activity. Occasionally the "fragments" appeared as univalents. However, more often, they appeared to be held together by a chiasma (Figure 1*A*, point a).

It is quite evident that the forces holding the "fragment" pair together at the chiasma (Figure 1*A*, point a) are greater than the point of union represented by the nucleolus organizer area (Figure 1*A*, points b, c, d).

The relationship of the fragment to the parent chromosome is without doubt a delicate one as evidenced by the ease of disarticulation. The position of the organizer area is similar to the situation in *Lilium*[15] in that it is not terminal. In the case of *A. pratensis*, a considerable portion of the chromosome arm extends beyond the organizer area and appears no different than the euchromatic remainder of the chromosome. Considering the apparent delicate heterochromatic continuity between the chro-

mosome proper and the "fragment" and considering the rather lengthy proportion of the "fragment", it would then not be too difficult to imagine disarticulation at this point as a result of cytological manipulation.

II. *Anthoxanthum odoratum*

Katterman[6] and Hunter[4] report fragment chromosomes in *A. odoratum*. Hunter reports two pairs of large fragments and one pair of small, almost spherical ones. They were always in pairs and never found as univalents. Parthasarathy[11] did not observe these fragments. However, he did observe that one pair of chromosomes definitely possessed a secondary constriction.

In the material of the present study, two pairs of satellited or secondarily constricted chromosomes were found (Figures 1*D* and 3 *B*). This agrees in part with Parthasarathy's findings. In addition, the chromosome arms in the present study often disarticulated at the secondary constrictions. These disarticulated satellites may correspond to the two pairs of large fragments observed by Hunter. The heteromorphic satellited chromosome 2 (Figures 3*B* and 1*D*, point b) did not disarticulate in our preparations. The distribution of this heteromorphic pair within the population was not determined, nor was meiosis studied in this species.

III. *Secale montanum*

Emme[2] reported *S. montanum* as having from one to two B-chromosomes. He paralleled this observation to the situation in 16 chromosome *S. cereale* as presented by Gotoh[3]. Gotoh demonstrated that the total chromosome length of the 16 chromosome rye was equal to that of 14 chromosome rye. He also identified cytologically the origin of the extra pair of chromosomes. Accordingly, Emme presented the *S. montanum* karyogram with the B-chromosome as having a theoretical origin similar to that shown by Gotoh in 16 chromosome rye. Lewitsky[8] disputed the origin of the extra pair of chromosomes as given by Gotoh; however, disregarding this controversy, the present evidence supports Emme's extension (in theory) of Gotoh's findings to *S. montanum*. From the idiogram (Figure 3*C*), it is evident that chromosome 4 possesses a large tandem satellite which when separated from the parent chromosome appeared as a supernumerary fragment (Figure 2*G*). The disarticulation of this chromosome, however, was not as frequent as was seen in *A. pratensis* or *A. odoratum*. Apparently the tandem satellite is so closely attached to chromosome 4 and the tertiary constriction so unpronounced that short arm and tandem satellite together appear as one long arm. This is clearly demonstrated in Figure 2*H* where the tandem satellite can be seen closely connected.

The tandem satellite of *S. montanum* resembles that of chromosome 14 of *Bromus haenkeanus*[13] and the B-chromosome of rye as observed by Tjio and Levan[17]. In these instances the short arms of the tandem satellites and the B-chromosome are "head" shaped.

Discussion

The present evidence indicates that the secondary constriction in *A. pratensis* (chromosome 5) is a very weak point. The very looseness of association of satellite to parent chromosome in this species suggests a mechanism whereby fragment chromosomes may be produced spontaneously, and possibly this situation represents an intermediate or near final stage in the development of this mechanism.

Therman-Suomaleinen[16] described in detail the secondary constrictions in *Polygonatum* species. Her observations in regard to the weakness of the chromosomes at these points is paralleled in the results of the present study. Similarly, Kaufmann[7] has observed in somatic mitoses of *Drosophila melanogaster* that the possibility exists that secondary constrictions may be quite tenuous and permit separation of the chromosome during smearing.

Three out of six *A. pratensis* plants studied herein did not have the easily disarticulated satellite. In these plants even the secondary constriction was not observable in root-tip chromosomes. This suggests the presence or absence of the weak secondary constriction to be facultative. The evolutionary implications of such a condition are several, but for lack of sufficient evidence a discussion is not in order at present.

In the field, *A. pratensis* is a highly variable plant and the plants used in the present study

did not include the entire range of variation. The species is self-sterile and its compulsory cross-pollination habit would tolerate cytological unbalances that might arise through inclusion of supernumerary fragment chromosomes. Since the plants used in the present study are not identical to those used by the earlier workers, the results herein would not necessarily infer a discrepancy.

Summary

Evidence presented indicates that the fifth chromosome of *Alopecurus pratensis* possesses a nucleolus associated tandem satellite which readily disarticulates at a secondary constriction during cytological manipulation and which could under casual observation be interpreted as a supernumerary fragment.

Two pairs of chromosomes with secondary constrictions were observed in *Anthoxanthum odoratum*. The four chromosomes were identical except for one whose secondarily constricted arm was one unit shorter than the comparable arm of the other three. The three identical chromosomes disarticulated regularly at the secondary constrictions and when the "fragments" were displaced, they appeared as supernumerary fragments.

In *Secale montanum* one pair of chromosomes was found to have secondary constrictions. Disarticulation did not occur as readily as in the above species; however, where it did occur, the "fragments" appeared as supernumerary fragments.

All of the species mentioned above have root-tip chromosomes with secondary constrictions. These constrictions are weak points at which disarticulation occurs during cytological manipulation. The fragments produced in this manner simulate supernumerary fragments. All of the above species have been described in earlier reports to have supernumerary fragments. It follows then that the earlier reports may be in part subject to error from this phenomenon.

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THE CRINKLED-FUZZY MOUSE.

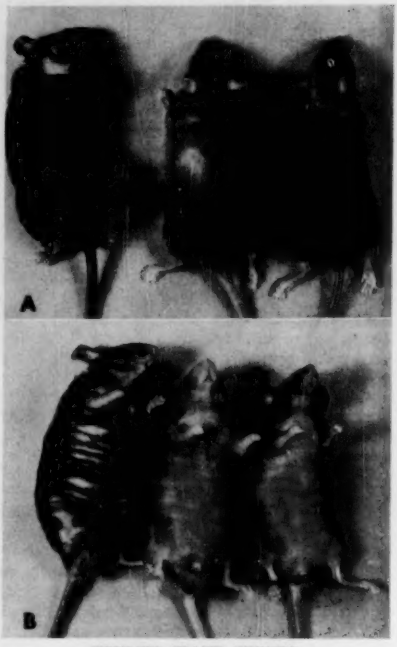
WILLYS K. SILVERS AND PRISCILLA W. LANE*

CRINKLED (*crcr*) is an autosomal recessive gene of the house mouse. The gene has many widespread morphological effects which have been described by Falconer *et al.*[3]. The most obvious effect involves the coat which is thin and abnormal in texture. As described by Dry[2] the coat of the normal mouse consists of monotrichs, awls, auchenes and zigzags. Auchenes are very variable in frequency, and often grade into awls through a transitional series of intermediates. For these reasons this hair type has not been considered as a type distinct from awls by Falconer *et al.*[3], nor will it be dealt with as a separate type in this paper.

The coat of crinkled mice consists entirely of awls. The development of the condition is accounted for by the failure of hair follicles to form between 14 and 17 days gestation and by a similar failure after birth. The coat of crinkled mice consists entirely of awls because these are the hairs formed between 17 days gestation and birth[3]. These awls are, however, histologically abnormal. The number of rows of medullary cells is not constant throughout the length of each hair.

Fuzzy (*fzfz*) is also an autosomal recessive gene of the house mouse described by Dickie and Woolley[1]. Animals of this genotype have curly coats which have been reported to contain "zigzag combinations"[1], quite different from any of the four types described by Dry[2].

If the fuzzy condition results in the absence of all hair types except those of the zigzag type, this gene would form a rough counterpart to crinkled. The double recessive (*crcrfzfz*) should, therefore, be completely naked[4]. It is also possible that rather than eliminating all hair types except zigzags, the fuzzy condition might alter the morphology of all hair types so that they resemble the zigzag combinations reported by Dickie and Woolley[1]. The purpose of this investigation was to make the necessary crosses to obtain the double recessive (*crcrfzfz*) in order to determine whether the fuzzy condition can be characterized as having only zigzag hairs.

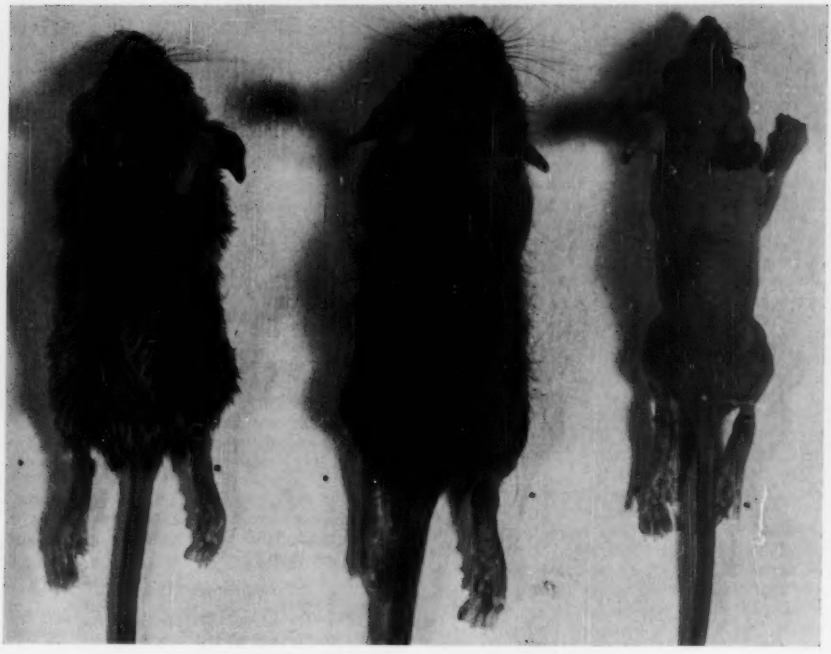


THREE HAIR TYPES

Figure 4

A and *B*—Dorsal and ventral aspects of crinkled, fuzzy and crinkled-fuzzy mice at 3½ months of age. Note reduction in the number of ventral hairs in the crinkled and crinkled-fuzzy mice. The crinkled and crinkled-fuzzy mice are black and the fuzzy mouse is leaden.

*The Wistar Institute of Anatomy and Biology, Thirty-sixth Street and Spruce, Philadelphia 4, Pennsylvania and the Roscoe B. Jackson Memorial Laboratory, Bar Harbor, Maine. Aided by a grant to the Jackson Laboratory from the American Cancer Society.



CRINKLED, FUZZY AND CRINKLED-FUZZY
Figure 5

Crinkled, fuzzy and crinkled-fuzzy littermates at 19 days of age. Note the retardation in growth and the naked appearance of the double recessive. At this stage the crinkled-fuzzy animal did exhibit a very short pelage. The crinkled mouse is leaden and the fuzzy mouse black. The coat color of the crinkled-fuzzy animal could not be determined when the photograph was taken.

Materials and Methods

Dickie and Woolley[1] reported that there had been two noticeable changes in the gross appearance of the fuzzy coat from the original type called "standard fuzzy." One change involved an intense curling of the hairs; the other increased the heaviness of the coat. No doubt these variations were the result of the expressivity of the fuzzy character on a heterogeneous background. These three fuzzy types have subsequently been selected for and maintained as three different stocks. The "standard fuzzy" type has been backcrossed for six generations into C57BL/6 animals and it is this type with which we are concerned.

A standard fuzzy (*fzfz*) female was mated with a crinkled (*crcr*) male. The F_1 animals from this cross were mated *inter se* and the segregant *crcrfzfz* mice were obtained. Dorsal hairs were plucked from both parental types and the F_2 crinkled-fuzzy mice. In addition, hairs of the snout region were plucked from the double recessive, since in young *crcrfzfz* animals this region exhibited the longest and heaviest pelage. The hairs were prepared for microscopic examination by the method of Russell[5].

Results

Crinkled, fuzzy and crinkled-fuzzy mice are shown in Figure 4. We were able to confirm the results of Falconer *et al.*[3] on the hair type of crinkled. This condition is characterized by the elimination of all hair types except awls. The awls of crinkled mice differ from awls of normal mice in that the number of rows of medullary cells is not always constant in the

main part of the shaft. Very few regions of crinkled hairs are more than two medullary cells in diameter and none appeared to be more than three. Many normal awls have regions which are four medullary cells in diameter at the broadest part. The hairs of the standard fuzzy coat were of the five types described by Dickie and Woolley[1]. In general the hair is much thinner than normal and faintly wavy. Some hairs were found containing regions which were two medullary cells in diameter with no constrictions indicating that the fuzzy animal may contain modifications of hair types other than the zigzag which has only a single row of medullary cells with several constrictions. This was borne out by the fact that the double recessive, *crcrfzfz*, was not hairless, exhibiting hairs on both the dorsum and ventrum (see Figure 4). As in the case of crinkled animals the ventrum contained much less hair than the dorsum. The crinkled-fuzzy mice displayed a slower growth rate than their crinkled or fuzzy littermates. The delayed eruption of hairs through the skin was very conspicuous. The growth of hair follicles was much more retarded than in the case of crinkled (Figure 5). The hairs plucked from the dorsum were very uniform. Microscopically dorsal *crcrfzfz* hairs had a single row of medullary cells with no constrictions. Hairs plucked from the snout region were either similar with those found on the dorsum, or resembled the hairs of crinkled animals since some contained regions which varied from one to two medullary cells in diameter.

Discussion

Animals of the double recessive, *crcrfzfz*, exhibit a pelage and therefore it does not seem possible that the fuzzy condition results in an elimination of all except zigzag type hairs. Moreover, the hairs which are found in the double reecssive are most probably modified awls since crinkled eliminates the other hair types. Awls are much more numerous on the dorsum than on the ventrum and this is undoubtedly responsible for the sparseness of hairs found on the ventrum of crinkled and crinkled-fuzzy animals. The uniformity of dorsal hairs on the *crcrfzfz* animal is a further indication that only one hair type, presumably awls, is present. These presumed dorsal awls are very different from both normal and crinkled awls. Some of the hairs located on the snout of crinkled-fuzzy mice are more similar to those present in crinkled animals. The fact that one double recessive affects the growth rate of the animal and the growth of hair follicles is interesting as it indicates genic interaction leading to pronounced pleiotropic effects. This deserves further investigation.

Summary

The question of whether the recessive gene, fuzzy, eliminates all hair types except zigzags was put to a genetic test by obtaining crinkled-fuzzy mice. Since crinkled eliminates all hair types except awls, the double recessive animal should be naked if animals of fuzzy genotypes contain only zigzags. The double recessive (*crcrfzfz*) contained hairs which although generally different from normal or crinkled awls were assumed to be of this hair type. It is concluded that fuzzy animals contain more hair types than zigzags.

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CLOSING DATE FOR RESEARCH PROPOSALS IN LIFE SCIENCES ANNOUNCED

The Division of Biological and Medical Sciences of the National Science Foundation announces that the next closing date for receipt of basic research proposals in the life sciences is May 15, 1958. Proposals received prior to that date will be reviewed at the Summer meetings of the Foundation's Advisory Panels and disposition will be made approximately four months following the closing date. Proposals received after the May 15, 1958, closing date will be reviewed following the Fall closing date of September 15, 1958.

Inquiries should be addressed to National Science Foundation, Washington 25, D. C.

INDUCED MUTATION OF POLYGENES FOR QUANTITATIVE CHARACTERS IN RICE

HIKO-ICHI OKA, JIRO HAYASHI AND ISAMU SHIOJIRI*

MUTATION of the so-called polygenes for quantitative characters might be a problem of wide interest for both geneticists and plant or animal breeders. The present writers tried to approach this problem from an irradiation experiment with a pure-line of rice (*Oryza sativa* L., a self-fertilized plant). The conclusion reached is that X-ray irradiation increases genetic variability, while the mean value of the irradiated populations remains unchanged, possibly due to the symmetrical occurrence of mutations with plus and minus phenotypic effects.

Materials and Methods

A pure-line of the variety "Kissin" (a commercial variety in western Japan), which was obtained by repeated self-fertilization from a single plant, was used. Seeds of a plant of the pure-line were divided into three parts; two of them were X-rayed at a dosage of about 6,000r (called XA-plot) and 12,000r (XB-plot) respectively, and the remaining one was left as the control.

The three plots were propagated in bulk from X_1 to X_4 in order to permit some of the mutations to become homozygous. The number of plants per plot was about 500. During these four generations, plants with any recognizable change, such as sterility, dwarfism, etc., were removed from the plots and were used for other purposes. Thus, only the plants with the normal appearance of the variety were retained in the populations.

Eighty X_4 plants were taken at random from each plot, and in the next X_5 generation, 75 of them were raised in pedigrees. They were tested by a split plot design (the main plot being the irradiation classes) with three replications. Each line (sub-plot) consisted of ten plants. Heading date and plant height were measured individually, but calculation was made on line mean basis.

In order to examine the effect of selection, ten extreme lines were selected (by line means averaged on three replications) in both high and low directions for each character from each irradiation class, and one plant was taken from each of the selected lines. Their progeny (X_6) were tested again by a similar split plot experiment with three replications.

The X-ray treatment was made in 1951 in National Taiwan University in Taipei, and the bulk populations up to X_4 were grown in Taiwan Provincial College of Agriculture in Taichung, Formosa. The field experiments were carried out in 1955 and 1956 at the Ohara Institute of Agricultural Research in Kurashiki, Japan, while calculation was done at the National Institute of Genetics, Misima, Japan.

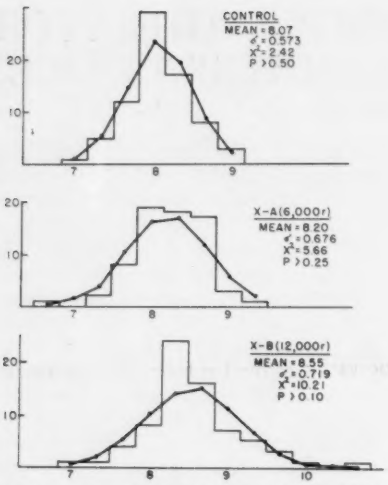
Presentation of Data

1. *The mode of frequency distribution in heading date and plant height*

The frequency distributions of line means averaged on three replications were examined. A normality test was made first in order to confirm the continuity of distribution.

As shown in Figures 6 and 7, the observed distributions gave good fits to the normal distributions which had been derived from the mean values and variances of the samples. Only a few lines outside the calculated normal distributions were eliminated from the populations to be studied. In plant height, all of the eliminated lines were dwarfs, while in heading date, they were either earlier or later than those within the range of normal distribution.

*National Institute of Genetics, Mishima, Japan (senior author), and Ohara Institute for Agricultural Research, Kurashiki, Japan, respectively. The authors are grateful for the kind help of their colleagues in Formosa and in Japan. Further, they appreciate the kind suggestions and advice of Dr. R. Takahashi of the Ohara Institute, Dr. M. Kimura of the National Genetics Institute, and Dr. J. F. Crow of the University of Wisconsin.



X-RAY AND CONTROL FREQUENCIES
Figure 6

Frequency distributions of line means in X-rayed and control plots for heading date (abscissa—days in September; ordinate—number of lines; histogram—observed; curve—calculated normal distribution).

The mean values and standard deviations found for each plot are given in Table I. It was found, as the data in Table I show, that the two irradiated and the control plots gave approximately the same mean, but they differed in variability; the XB-plot (12,000r) showed the largest, the XA- plot (6,000r) intermediate, and the control the smallest standard deviation in both characters investigated, and the differences among them were statistically significant.

2. *Estimation of genetic and environmental components of variance*

The results of variance analysis of the data for X_5 lines are given in Table II. As seen in the table, it was found that variances of line means were statistically significant in all plots, although the irradiated plots tended to have larger F values than the control.

The values of genetic and environmental components of variance calculated from the data in Table II, in terms of the values to be expected on an individual plant basis, are given in Table III. It is recognized in Table III that the genetic component, although smaller than the environmental component, tends to increase with the dosage of X-rays.

Assuming that the increase of genetic variance due to radiation is proportional to the dosage, the rate of increase per kilo-roentgen was computed as shown in Table III. If expressed as an increase of standard deviation, the rate is approximately 0.124 days/Kr for heading date, and 0.29 cm/Kr for plant height.

3. *A selection experiment*

As has been stated, ten extreme lines were selected in both high and low directions for each character from each of the irradiation classes, and the parent-offspring regression was calculated for each of them. The heritability values thus found for both heading date

TABLE I. Mean values and standard deviations in X-rayed and control plots

a) Plot means for heading date (days in September)

Plot	Mean value 1	2	3	Average	Standard deviation 1	2	3	Harmonic Mean
Control	7.49	7.87	8.85	8.07	0.679	0.500	0.524	0.573
X-A	8.29	8.09	8.19	8.19	0.790	0.614	0.606	0.676
X-B	8.31	8.70	8.56	8.52	0.762	0.678	0.705	0.719

b) Plot means for plant height (cm)

Control	112.7	112.4	113.6	112.9	1.876	1.661	1.650	1.732
X-A	113.7	112.3	114.4	113.5	1.976	1.578	1.973	1.852
X-B	113.9	113.4	113.4	113.6	2.916	2.006	2.019	2.076

c) Variance analysis of the data

Source of variation	d.f.	Heading date Mean	Heading date Standard dev.	Plant height Mean	Plant height Standard dev.
Replication	2	0.193	0.019,5	1.019	0.053,7
Treatment	2	0.165	0.017,2**	0.402	0.092,6*
Error	4	0.175	0.001,3	0.340	0.013,8

*Between 1% and 5% levels of significance.
**Beyond 1% level of significance.

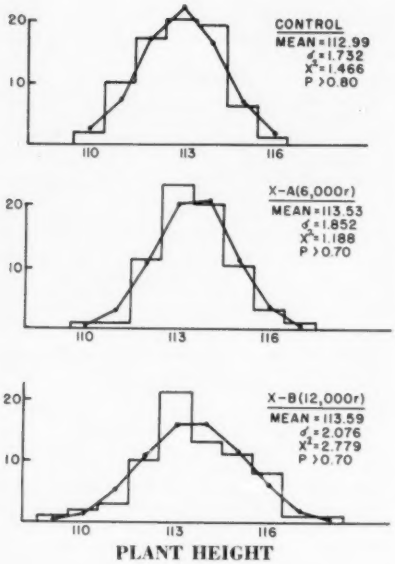


Figure 7

Frequency distributions of line means in X-rayed and control plots for plant height. (Abscissa—height in cm; ordinate—number of lines.)

and plant height are given in Table IV.

The statistical significance of heritability values given in Table IV was obtained from the significance of regression coefficient. The table shows that in plant height selection was effective only in the X-rayed plots, and in heading date it was effective in all plots, though the X-rayed ones had higher values than the control. The existence of significant heritability in the control plots might be explained by natural increase of genetic variability possibly due to spontaneous mutations during bulk propagation or residual heterogeneity.

Discussion

It is our present knowledge that quantitative characters are generally controlled by the so-called polygenes, which are a series of genes whose individual effect is smaller than the range of environmental variation. They are considered to be of great importance in breeding and in evolution of plants and animals. However, how the polygenes respond to irradiation seems to have been an unexplored problem. Irradiation experiments with crop plants have been carried out mainly for breeding purposes. Though mutants are mostly deleterious, successful results in finding "good mutations" have been reported by several workers: Gustafsson[3] in barley, Gregory[2] in peanuts, and others. Polygenic mutations might have been involved in the induced genetic variability dealt with in these works.

In the present experiment, all individuals with recognizable changes were removed and only the lines coming within the range of normal distribution were used for study. They appeared in the experimental field to be completely normal and uniform. Therefore, the increase of genetic variability detected in the present experiment should be considered to be due to polygenic mutations. As far as the present experiment goes, our conclusion is rather simple: The population mean does not change, while genetic variability within the populations increases due to irradiation. This may suggest that by irradiation polygenic mutations with plus and minus effects occur equally frequently in both directions.

It is well known, in contrast, that mutations in the so-called major genes mostly bring about a break-down of some metabolic pathway, and a skewed phenotypic variation results. If our finding for polygenic mutation is valid, the symmetrical augmentation of phenotypic variation may be considered to be characteristic of mutations in polygenes for a quantitative character. Dr. A. B. Burdick of Purdue University kindly told one of the writers (Oka) that in his unpublished data with *Drosophila* he has also found a symmetrical increase of

TABLE II. Analysis of variance of line means in X-rayed and control plots

Treatment	Variation due to	d.f.	Mean squares (and F values) Heading date	Plant height
Control	Lines	74	0.508**(2.1)	4.232* (1.5)
	Error	148	0.239	2.914
X-A	Lines	69	0.784**(2.7)	4.788**(2.3)
(6,000 r)	Error	138	0.293	2.107
X-B	Lines	70	1.061**(4.5)	8.210**(3.5)
(12,000 r)	Error	140	0.238	2.358

*Between 1% and 5% levels of significance.
**Beyond 1% level of significance.

variability in quantitative characters due to irradiation.

Clayton and Robertson[1] reported that in abdominal chaetae number of *Drosophila*, X-rayed populations showed greater responses to selection in both high and low directions than non-X-rayed populations. They computed the increase of genetic variance from the heritability values obtained from the data. It was pointed out by Scossiroli[4] that populations of *Drosophila* that had reached a plateau responded again to selection after irradiation. These experiments indicate that polygenes mutate due to radiation, resulting in an increase of genetic variability.

In these as well as our experiments on polygenes, however, it seems difficult to estimate the number of related genes and their individual effects on phenotypic expression. It is then difficult to measure the mutation rate for individual genes. As pointed out by Clayton and Robertson[1] dealing with quantitative characters, the rate of increase of genetic variance may stand for the mutation rate for genes with major effects. Our estimate of this rate is given in Table III, in terms of the rate of increase per kilo-roentgen.

Theoretically, the increase of genetic variance may be accounted for as ku^2, where k is the number of relevant loci, u is the average mutation rate, and d is the average individual effect. The mutations dealt with in the present study were unrecognizable in the experimental field. We may take the average effect d to be one-half of the standard deviation for environmental variance. Then assuming 100 loci, we find the mutation rate to be 2.4×10^{-4}/Kr for heading date, and 1.4×10^{-4}/Kr for plant height. These values might be rather comparable with the mutation rates so far known.

TABLE III. Genetic and environmental components of variance to be expected on an individual plant basis

Variance component	Heading date (day)	Plant height (cm)
Environmental	2.567	24.594
Genetic,		
Control	0.084	0.591
X-A (6,000r)	0.176	0.776
X-B (12,000r)	0.268	1.917
Rate of increase per 1,000r	0.015,3	0.083,9

TABLE IV. Heritability values estimated from selection experiment

Character	Control	X-A	X-B
Heading date	0.201**	0.239**	0.321**
Plant height	0.106	0.296**	0.220**

**Beyond 1% level of significance.

Summary

Three experimental populations, control and two X-rayed (6,000r and 12,000r), were prepared from a pure-line of rice. They were propagated in bulk up to the X_4, and during these generations, plants with any recognizable change were removed from the populations. Seventy-five X_5 lines were raised by random sampling from each population, and were investigated by a split plot design experiment with three replications regarding heading date and plant height. Measurement was taken on an individual plant basis, but line means were used for calculation.

In each plot, lines coming within the normal distribution calculated from the mean value and variance of the samples were used for study. They appeared in the experimental field to be quite normal and uniform. It was pointed out that the three plots, control and two X-rayed, did not differ significantly in mean value, while the variability within plots increased due to irradiation. This suggests that mutations with plus and minus effects have occurred approximately equally frequently. The increase in genetic variability was computed from the component analysis of variance, and was given in terms of the rate of increase of genetic variance per kiloroentgen.

Ten extreme lines were selected from the X_5 populations in both plus and minus directions for each character, and the descendant X_6 lines were tested again with three replications. Plots which had received higher dosage of X-rays tended to have higher heritability values.

It was concluded that, as far as the present study goes, mutations of the so-called polygenes brought about a symmetrical increase of variability in both high and low directions.

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LYSENKO AT BAY

THEODOSIUS DOBZHANSKY*

FAILURE to recognize that the behavior of people is liable to be tantalizingly self-inconsistent easily leads to misconception. The elevation of Lysenko to dictatorship over Russian biology and agriculture seemed to many a proof of collapse of all science in Russia. Could anything but degradation result from replacement of science by quackery in the direction of biology and agriculture? If a blunder so egregious had been committed in biology and agriculture, could reason prevail in other fields? The disrepute which Lysenko brought on Russian science will not soon be forgotten. And yet a series of events, culminating thus far in the launching of artificial satellites, have shown that Lysenko is not a fair indicator of the level of Russian science as a whole. A prominent American scientist has now suddenly discovered that "Russians, man for man, are as educable as Americans are."

The high standing of physical and engineering sciences in Russia is evidently not incompatible with Lysenkoism. To be sure, Lysenko is no longer the lord that he once was; but neither is he hors de combat. His rise, beginning about 1930, was due to the increasingly determined backing which he received from political authorities. He never had any support from scientists, since not much understanding of biology was needed to recognize the spurious nature of his pretended discoveries. However, no criticism was permitted, and in August of 1948 Lysenko uttered the proud words: "The Central Committee of the Party has examined my report and approved it."

Lysenko's uncontested reign lasted less than four years. The first, very tentative, dissent appeared in 1952 in *Botanichesky Zhurnal*, a botanical periodical published by the Academy of Sciences of USSR. Since then, many critics, in this and in other publications, have pretty well demolished the whole "progressive Michurinist biology." This is, of course, not difficult to do, provided only that those who undertake the unpleasant task can express freely their opinions. That this is not the case is evident from reading even the most outspoken criticisms yet published in USSR. Michurin remains an indisputable authority, and rather pathetic attempts are usually made to show that Lysenko did not follow Michurin as fully as he should have done, rather than to question Michurin's own dicta. It is, therefore, only natural that outspoken refutations of the once sacred doctrine of Michurinism-Lysenkoism have been published by communist authors on this side of the Iron Curtain. Thus, Professor Marcel Prenant, the author of "Biologie et Marxisme," who for a time occupied a somewhat equivocal position with respect to Lysenko's claims, has now made a clean break with Lysenkoism.†

Lysenko is, however, not a man to accept defeat without last ditch resistance. In a long article in the official organ, *Izvestia*, he makes a bid for reinstatement in the official favor.‡ Both the contents and the form of this article give unusually clear insights in the workings of the mind of a high Soviet official desperately fighting for his position of power.

The gist of Lysenko's argument, reiterated again and again throughout the whole long article (almost a page in the 6-page newspaper), is that the "Michurinist doctrine" is helpful to practical

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†Prenant, Marcel. Biologie et Marxisme. Hier et Aujourd'hui, Paris (1948). (See my review in the *Journal of Heredity*, 40:78-79. 1949)—Prenant, Marcel. Les problems biologiques. *La Pensée* 72: 23-26. 1957.

‡Lysenko, T. Theoretical attainments of agricultural biology. *Izvestia*, No. 290, December 8th, 1957.

agriculture, while genetics is allegedly worthless in this respect. "For example, it is very important to know whether it is very important to know whether it is possible to control the heredity of agricultural plants and animals. Can one modify it in the direction of usefulness? The classical genetics, which is the Weismannian genetics, gives a clear answer: It is not possible to obtain directional changes in the heredity of organisms. Michurin, and his Michurinist followers, on the basis of the materialist understanding of living nature, maintain that directed changes of heredity can be obtained. . . ."

It would be too much to expect most readers of *Izvestia* to be able to detect the adroitly concealed deception in the above statement. Directed mutations in agricultural plants and animals are not yet within reach, but surely no geneticist has ever doubted the possibility of modifying the heredity of these organisms in the direction of usefulness by scientifically conducted selection, aided by hybridization and perhaps by mutation to increase the genetic variance. This is precisely what scientific plant and animal breeders are doing, and with no mean success.

The genteel art of quoting out of context whatever suits them, and interpreting the quotations without regard to their authors' meaning, has been successfully used by Lysenko and his followers. The Master has not yet lost his art. We read in Lysenko's article that the eminent Swedish geneticist Gustafsson favors scientists concealing some of their findings, while the French biologist Jean Rostand is represented, on the contrary, favoring full publication and wide dissemination of scientific facts, no matter how embarrassing they may be. What Gustafsson actually wrote is that outside Russia anybody who would publish anything like Lysenko's "theories" would be laughed down, and Rostand expressed grave doubt about the validity of Lysenko's alleged discoveries.

I. M. Lerner, the California geneticist, is quoted as follows: "It is perfectly clear that if these experiments [on 'vegetative hybridization' in poultry] could be repeated on pure-bred material outside the territories of the Soviet Union and of its allies, then no geneticist anywhere will be able to deny Lysenko's theories." The condition made by Lerner is, of course, highly unreasonable; however, it has been fulfilled anyway by the recent experiments of Benoit in France on the induction of mutations in ducks by DNA transforming principles. It is again safe to assume that a great majority of the readers of *Izvestia* will not know that Benoit's experiments are themselves in need of verification, and that Benoit's results have anyway not the remotest bearing on the kind of "vegetative hybridization" which Lysenkoists have claimed to have made in poultry and elsewhere. But Lysenko understandably dislikes to mention that extensive and careful repetition of his experiments by Stubbe, in East Germany, has wholly failed to confirm the results by Lysenko.

Hybrid corn remains, to date, the most important practical attainment of genetics. Here Lysenko has to tread gently, for this product of bourgeois genetics has won the favor of some very powerful persons in USSR. So, Lysenko uses for an ally none other than the distinguished American corn geneticist F. D. Richey! The initiation of the work on hybrid corn is rightly credited to the late G. H. Shull, but Shull's interpretation of heterosis was, according to Richey, non-Mendelian. Q. E. D.! Purely as a sleight of hand this trick is well done!

The true nature of heterosis has been discovered, according to Lysenko, by the Michurinists. In Lysenko's crystal clear language the discovery is described thus: "In the Michurinist biological doctrine the viability is understood to be a result of the contradictions in the living body. The degree of the contradictoriness, and hence of the viability of a living body, depends to a certain extent on the degree of the qualitative oppositeness. On this foundation, various methods of increasing the viability of plant and animal organisms have been and are being developed."

No less impressive is the solution of one of the basic problems of theoretical biology—the problem of species. This is as follows: "On the basis of the modified and deepened materialist elements in the teaching of Darwin, the biological teaching of the Michurinist school has discovered that all biological spe

cies are qualitatively determined links of living nature, which live and develop on the basis of a single law of the life of species. The essence of the law of life of biological species is manifest in the directedness of life processes towards increasing the living mass, not the living mass in general but that of a given concrete species. Hence, in a normal, non-pathological, living body all the structures and states, all the properties and processes, all the diverse requirements of living conditions, all the diverse reactions on the influences of the not-needed, foreign, conditions of the external environment—all this is in various ways directed towards increasing the mass of this given, concrete, biological species, even if this shortens the life of a given concrete individual, and even if this results in its natural death."

Some leaders of the *Izvestia* will perhaps be impressed by the depth of this deepened teaching, though others may wonder why it needs to be stated with such grammatical incoherence. But probably not many will see what is hidden under the verbiage. Even at the beginning of Lysenko's fame, the late G. B. Shaw proclaimed, possibly with tongue in cheek, that the vaunted dialectical materialist Lysenko was really a disguised vitalist. Shaw was closer to the truth than he may have realized. Lysenko's "single law of the life of species" is a restatement of his two startling discoveries first announced apparently in 1945. One discovery was that the organism possesses a sort of an unconscious racial memory, which enables it to draw from its environment just those materials (or "conditions" as Lysenko prefers to call them) which enabled its ancestors to develop successfully. This notion was propounded some 80 years ago by Darwin's critic Samuel Butler, and especially by the German vitalist R. Semon early in the current century.

Lysenko's second discovery was his denial of competition between individuals of the same species. Conspecific individuals do not act as each other's rivals even when the population density and the food supply become limiting factors in survival. Most individuals allegedly sacrifice themselves in favor of one or more lucky ones who will be able to survive with the resources available. This may seem to be Lysenko's one original idea, though a mighty strange one for a professed materialist. But Prenant has pointed out in the article cited above that this idea was debated by Bernardin de Saint Pierre, one of most extreme teleologists of the eighteenth century. This does not mean that Lysenko consciously plagiarized from Butler, Semon and Bernardin de Saint Pierre. Most likely he never heard their names. Neither was he necessarily a plagiarist when he announced as his own idea Darwin's long since disproved "provisional hypothesis of pangenesis." But these coincidences are characteristic. What they do mean is that Lysenko's "progressive biology" stands on the level of understanding of nature characteristic of the nineteenth, or even the eighteenth, centuries. As pointed out particularly by Conway Zirkle, the belief that acquired characters are inherited is not a generalization of any scientific facts but a part of pre-scientific folklore.

During the years of his unchallenged power, Lysenko was careful to fill most of the influential posts in academic and research biology and agriculture with his followers. A body of vested interest has been created. Lysenko's followers do their best to support Lysenko for the sake of their own survival. Moreover, the propaganda machinery of the state has persuaded masses of people that Lysenko was an innovator in science and a figure of almost heroic proportions. Almost a whole generation has learned whatever biology it did learn from books and from teachers who glorified the "progressive Michurinist science." It is not surprising that Lysenko is still able to command space in the *Izvestia*, although no longer able to silence all his critics. The failure of Lysenkoism is no longer a secret to many people even in Russia, not to speak of the rest of the world. A hodge podge of folk tales can be substituted for science only by force of repression, and then only for a while. It cannot stand criticism, even half-free criticism. Lysenko is fully aware of this.

TRACER STUDY OF POLLEN-TUBE GROWTH IN CROSS-STERILE MAIZE

L. R. HOUSE AND O. E. NELSON, JR.*

THE fourth chromosome gametophyte locus (Ga_1) in maize has been the most extensively studied of the seven gametophyte loci known. Ga_1 gametophytes have almost a complete advantage over *ga* gametophytes in effecting fertilization when both types are competing on Ga_1/Ga_1 or Ga_1/ga plants. Emerson was the first to identify this *gametophyte* factor[3], and he reported that the *gametophyte* locus was linked to the sugary locus with 28 percent recombination[4]. The possible mechanisms of action of differential pollen-tube growth were first considered by Mangelsdorf and Jones[6] and Mangelsdorf[7]. Demerec[2] reported a case where *ga* pollen failed to induce seed set even in the absence of competing gametophytes. Schwartz[9] working with a case similar to that of Demerec concluded that there was a third allele Ga^s at the Ga_1 locus. On Ga^s/Ga^s plants *ga* gametophytes fail to induce a seed set. Schwartz demonstrated that *ga* pollen grains did germinate on Ga^s/Ga^s styles and grew into the style. Nelson[8] extended these observations showing that *ga* and Ga^s pollen grains both germinated at the same rate on Ga^s/Ga^s styles and that growth into the styles was similar as far as could be followed (into the vascular strands traversing the length of the silk). Nelson presented evidence ruling out the possibility that after an incompatible pollination fertilization failed at the ovule or that the developing zygote collapsed. He believed that the sterility reaction was one between the diploid style and haploid pollen-tube and suggested that the sterility reaction might involve nutritive difficulties or be of an immunological type; i.e., antibodies are formed in response to an antigen introduced by the pollen-tube.

A cytological examination as an aid in studying the physiology of pollen-tube development is tedious[1]. The following includes a description of an autoradiographic technique used to study the development of Ga^s and *ga* pollen-tubes in Ga^s/Ga^s-styles.

Materials and Methods

The cross-sterile stocks (Ga^s/Ga^s) used as seed parents were the popcorns 1001-52 in the 1955 field planting, and (842-L × D3-6) in the 1953-54 greenhouse experiment. The inbred 1001-52 is a Hulless type; 842-L is from Ohio Yellow and D3-6 is a South American inbred. Radioactive pollen parents were 1001-52, Hy, and P51 in the field planting, and (842-6 × D3-6) and US 13 in the greenhouse. The inbred Hy is from Illinois High Yield dent corn, P51 is a sweet corn and US 13 is a dent hybrid; these three types are *ga/ga* in constitution.

High specific activity phosphorous-32, a *beta* emitter, was used as the phosphate ion in dilute hydrochloric acid. The dose of the isotope administered to the plant varied with the plant size; those less than five feet received one-half millicurie while those greater in height than five feet received one millicurie. Using such dosages the activity of the pollen obtained should have been more comparable than if the dose had been constant. The radioactive solution was injected from a radiation-protected syringe into a well bored into the plant stem just below the ear-bearing node. Injections were made just as the tassels first began to shed pollen.

Activity in the pollen was first recorded about 25 hours after injection and then rose rapidly (Figure 8). Pollen

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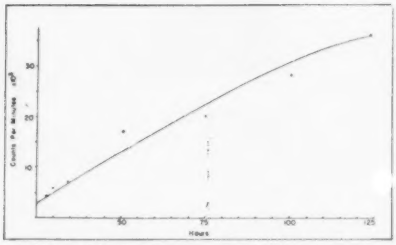


PHOSPHOROUS-32 ACCUMULATION
Figure 8

Accumulation of phosphorous-32 in the pollen plotted as counts per minute per 50 milligrams of pollen against the time in hours after injection of the phosphorous.

was sufficiently radioactive for use two days after the plants were injected. The radioactivity of the pollen continued to rise as long as the tassel shed, but never exceeded one count per minute per pollen grain.

Radioactive pollen was dusted onto an even "brush" of silk obtained by cutting the silks back to the husk tip the day before pollination. Germination and growth of the pollen-tubes in the style was allowed to proceed for varying periods of time (see Table I). After a designated time interval the ear was harvested and the "brush" of silk again cut back to the husk tip in order to prevent ungerminated "hot" pollen from contaminating stylar material from husk tip to ovule when the husk was cut open.

Wedge shaped sections of the cob with ovules and silks attached were removed from the ear in a place away from the radioactive plants. The tissue was killed by drying. FAA (formalin, acetic acid, alcohol) was tried as a killing agent, but too much leaching of phosphorous occurred to afford satisfactory autoradiographs. The sections were laid out in a blotter paper press within a few minutes of harvest, and killing should have occurred soon after. The tissue sections were allowed to remain in the press until they were dry enough not to adhere to the X-ray film.

The sections were mounted on 14 × 17 inch glass plates using shellac diluted with two or three volumes of alcohol as the adhesive. The glass plates were placed in direct contact with the X-ray film. Exposure was allowed to proceed for six weeks.

*Radioactive pollen.

Results and Discussion

The length of the white streaks on the photographs (Figures 9 and 10) are proportional to the distances which the pollen-tubes grew in the sections of style sampled. Phosphorous-32 is distributed along the whole length of the tube. The streaks were measured and a correction was made for the length of silk removed before opening the husk. The means of the measures for each ear was obtained, and the weighted mean for all ears sampled for each collection time is presented in Table I.

The variation within a sample is on the average rather small, one standard deviation being in the neighborhood of 2.0 millimeters. However, the variation between samples for each time period is quite large as can be observed in the range column of Table I. Because of the high variation it is possible only to suggest the nature of several aspects of the cross-sterility reaction.

Two compatible crosses were made as follows—1001-52 × 1001-52* (Ga^s/Ga^s) in 1955 and (842-L × D3-6) × (842-L × D3-6)* (Ga^s/Ga^s) in 1953. No differences were observed between these two crosses and the results were pooled. If growth in millimeters

TABLE I. Growth of compatible (Ga^s)* and incompatible (ga)* pollen-tubes in Ga^s/Ga^s styles as determined by the autoradiographic technique

Time	Ears pollinated	Total silks measured	Average growth	Range
hrs.	no.	no.	mm.	mm.
		x Ga^{s*}		
2	4	40	19.3	17.3- 24.5
4	4	111	47.2	30.9- 53.1
8	4	65	94.5	66.8-107.7
		x ga^*		
2	1	1	17.0	
4	3	94	19.0	15.4- 24.1
8	5	104	33.4	24.2- 47.7
12	3	79	15.7	9.3- 20.9
16	2	37	27.6	24.4- 31.4
22	2	48	31.7	30.7- 32.6
24	2	46	17.3	17.1- 17.6
30	2	38	23.5	19.6- 25.8
38	1	18	24.4	
48	5	34	38.5	25.3- 46.8

*Radioactive pollen.

DEVELOPMENT OF POLLEN TUBES
Figure 9

Autoradiographs showing development of pollen-tubes in Ga^s/Ga^s silks. *A-C*—Ga^s pollen tubes at two, four, and eight hour periods of growth.

is plotted against time in hours, the curve from the 2 to 8 hour period is linear. The slope of the curve indicates that the growth rate is about 12 millimeters per hour. The information beyond the eight hour period is unreliable because the pollen-tubes in many cases grew through the style (usually between 110 and 140 millimeters) before the end of the growth period; therefore, these date are not presented.

Two incompatible crosses were made, 1001-52 × Hy* (*ga/ga*) or P51* (*ga/ga*) in 1955 and (842-L × D3-6) × US 13* (*ga/ga*) in 1953, and as no differences in pollen-tube growth were apparent the results were pooled. It can be observed from Table I that incompatible pollen-tube growth continued for about four hours then ceased somewhere between the four and eight hour period. After four hours, the pollen-tubes averaged 19.0 millimeters in length, and the average of all values from the eight to the 48 hour period was 27.6 millimeters. After eight hours no further growth was observed. It is also of interest to note that at no time did incompatible pollen-tubes on an average grow as far as the compatible pollen-tubes indicating that the growth rate of the incompatible tubes was seldom equal to that of the compatible tubes. Apparently the reaction resulting in sterility begins shortly after germination and inhibits growth more and more until development ceases.

The inbred 1001-52 was pollinated on one day with nonradioactive *ga* pollen from either P51 or Hy. The following day the same silks were pollinated again, but with 1001-52* pollen. The information available is scanty (Table II), but there are indications that the previous incompatible pollination had no effect on the subsequent compatible pollination. Whatever the nature of the antagonism resulting from the sterility reaction, there is apparently no effect on compatible pollen-tubes growing in the style one day after incompatible pollen-tubes.

In an experiment similar to the above, except that the second pollination was with *ga** pollen, the results indicated (Table II) no significant differences between this type of cross and the type 1001-52 × *ga**. The high variation and short growing distance obscured any small differences that might be present. Apparently, one day after an incompatible pollination, there is no effect (as a result of the first pollination), on pollen-tubes of a second incompatible pollination.

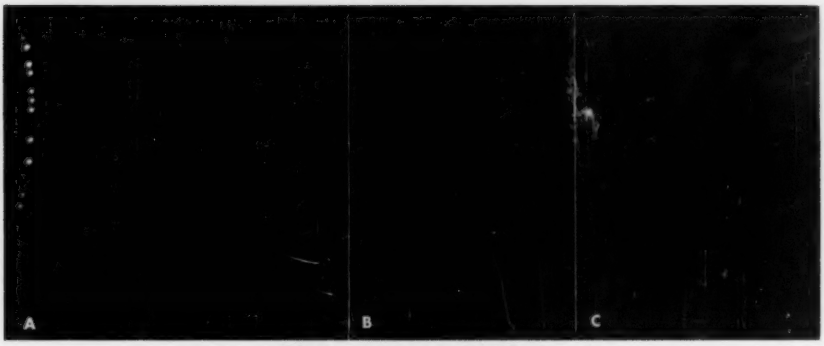
The streaks on the photographs (Figures 9 and 10) are much more pronounced in the case of a compatible pollination indicating that a greater number of pollen-tubes traversed the

TABLE II. Growth of compatible (Ga^s)* and incompatible (*ga*)* pollen-tubes in Ga^s/Ga^s styles one day after an incompatible pollination (*ga*)

Time	Ears pollinated	Total silks measured	Average growth	Range
hrs.	no.	no.	mm.	mm.
		x Ga^s*		
4	2	38	31.7	25.1-40.8
8	1	35	136.4	
		x *ga**		
4	4	116	25.7	20.5-35.0
8	2	46	29.0	28.5-29.5
24	2	43	22.8	16.5-27.6

*Radioactive pollen.

*Radioactive pollen.



THREE GROWTH PERIODS

Figure 10

Autoradiographs showing development of pollen tubes in (*A*) *Ga*^{s} pollen tubes, 16 hour growth period. *B* and *C*—*ga* pollen tubes, four and eight hour growth periods.

silk after a compatible pollination than after an incompatible pollination. Apparently the majority of incompatible pollen-tubes ceased development very soon after germination. Phosphorous-32 in the ovules is apparent in the case of *Ga*^{s}* pollinations after eight and 16 hour growth periods (bright spots on the photographs).

Summary

An autoradiographic technique has been presented which has been of value in the study of the development of compatible (*Ga*^{s}) and incompatible (*ga*) pollen-tubes growing in *Ga*^{s}/*Ga*^{s} silks.

The growth of compatible pollen-tubes appears to be linear with time and at a rate of about 12 millimeters per hour.

The development of incompatible pollen-tubes apparently ceases after eight hours, and evidence is presented that the growth rate is seldom equal to that of compatible pollen-tubes. Apparently the incompatibility reaction begins with pollen-tube growth, and the growth rate continually slows down until development ceases.

There is an indication that an incompatible pollination has no effect on pollen-tubes, either compatible or incompatible, growing through the same silk one day later.

A larger number of compatible than incompatible pollen-tubes grow in the style.

*Radioactive pollen.

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STUDIES ON DDT-RESISTANCE IN DROSOPHILA MELANOGASTER

From the Viewpoint of Population Genetics

CHOZO OSHIMA*

THE results obtained by previous authors concerning the genetics of insecticide resistance in *Drosophila* disagree in some essential points. This may be partly due to differences in material and partly to methods used in their experiments. For instance, Tsukamoto and Ogaki[13,14,15] have concluded that DDT-resistance in *D. melanogaster* is controlled by a single dominant gene located on the second chromosome, while Crow[1,2,3] and King[6,7] maintain that many dominant and recessive factors located on almost all chromosomes are involved.

In *Drosophila* no DDT-resistance as high as seen in the house-fly has been demonstrated and biochemical study on mechanisms of detoxifying the DDT effect have not been performed. As Hoskins and Gordon[4] have pointed out, vigor tolerance may have some relation to the resistance, in addition to specific factors which affect DDT-detoxification. The experiment described in this paper was carried out from the viewpoint of population genetics. The regression of resistance with relaxation of DDT selection and the interaction between genetic factors related to resistance are discussed.

Materials and Methods

Four strains, H, K, C and *sca;ss*^{a}, were used. Flies of the H-strain were collected in Hikone City in 1952 and have since been cultured in our laboratory. They have shown high resistance to DDT and also to several other insecticides. Flies of the K-strain were collected in a small uninhabited island in the Japan Sea in 1951 and have been inbred in our laboratory. Their resistance to DDT is moderate. The C (Canton-S) strain has been kept over a long period of time in our laboratory and has been shown to be susceptible to DDT and also to some other insecticides. The *sca;ss*^{a} strain is homozygous for the recessive

TABLE I. The percentage of mortality of each original and marker strains and their F_1 hybrids

Original strain	Mortality (%)	Marker strain	Mortality (%)
H (Hikone)	1.3	*sca ; ss*^{a}	67.3
K (Kanmurijima)	28.0		
C (Canton-S)	100.0		

F_1 hybrids	Genotype	Mortality (%)
sca ; ss^{a} × H	$\frac{sca \quad ss^{a}}{+} ; \frac{}{+}$	15.0
sca ; ss^{a} × K	"	22.3
sca ; ss^{a} × C	"	89.0

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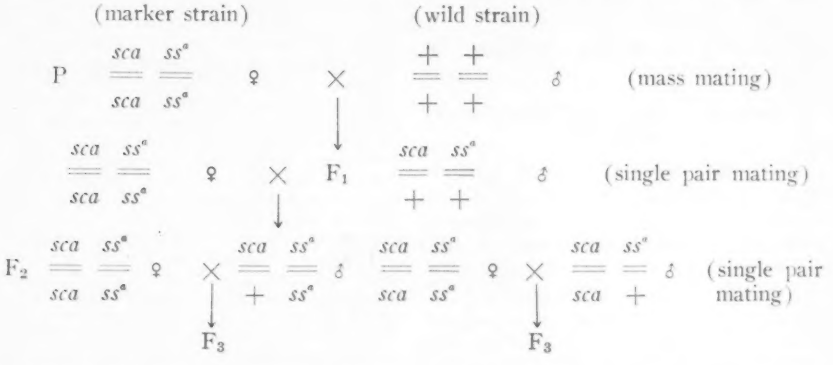
mutant genes, *sca* (scabrous-rough eye) and *ss*^{a} (spineless aristopedia-abnormal bristle and antennae) located on the second and third chromosome respectively, and shows a slight susceptibility. The comparative resistance of these strains is shown in Table I.

As the first step in deriving experimental populations, crosses were performed as shown in the following mating scheme:



Each wild strain was crossed with the marker strain by mass mating and the crosses in the following two generations were performed by single pair matings. In the F_2 generation, four different phenotypes were obtained. The female flies, homozygous for *sca* on the second and *ss*^{a} on the third chromosome and the male flies, homozygous for one of these chromosomes and heterozygous for the other, were chosen and crossed by a single pair mating. Twenty virgin female flies carrying two mutant characters and 20 male flies carrying one mutant character from the F_3 generation were introduced into a bell-shaped glass cage. These flies formed the initial population of the experiment.

The cage had a cork bottom with four holes in each of which a glass tube containing the culture medium was inserted. The culture medium consisted of malted rice, sugar, agar and yeast and no DDT. Two tubes were replaced every two weeks with fresh food.

In the F_1 backcrossing, two sets of single pair matings were prepared from each of the six parental crosses. Thus, there were 12 initial populations cultured in the cages. These populations will be called the "analytical" populations. Only six, one of each type, were finally analyzed. The object of preparing these analytical populations was to find the level of DDT-resistance due to the presence of a major autosome from a resistant strain and to follow the change in resistance in the following generations in a DDT-free environment. The frequency of a resistance gene in each population was assumed to be about 25 percent. The frequency of the *sca* gene in the analytical populations of the flies carrying the second chromosome derived from the wild strain gradually decreased to less than five percent after one year cultivation. In the other populations, the frequency of the *ss*^{a} gene decreased even more rapidly. In the initial populations, the genes responsible for DDT-resistance were heterozygous. The resistance of all analytical populations was measured at intervals, in order to see what kind of change in resistance had occurred in the DDT-free environment.

After a period of cultivation, two kinds of analytical populations, one in which the frequency of the *ss*^{a} gene had decreased by natural selection and the other in which the frequency of the *sca*

gene had decreased, were mixed together and cultured in a population bottle without DDT. These populations will be called "synthetic" populations.

The mutant genes in these populations gradually decreased by natural selection as in the analytical populations. At the same time, other synthetic populations, having the same genic constitution, were cultivated in a medium containing DDT. The object of this experiment was to confirm whether or not the frequency of genes responsible for the DDT-resistance would increase by DDT-selection.

Method of Testing DDT-Resistance of Adult Flies

Five pairs of flies, taken at random from a population, were kept in a bottle for three days. Their offspring were collected on emergence from cultures which were not overcrowded and held for four or five days before testing. The degree of resistance was determined from the mortality of the flies exposed to DDT for 24 hours. Fifty adult flies were introduced into a glass tube stoppered with a cotton plug. A piece of filter paper treated with DDT (25 γ/cm^2) from an acetone solution was pasted with starch to the bottom of the tube. The tube was placed in a large dessicator in which the humidity was maintained at 75 percent and the temperature at 25°C. The mortality was determined by repeating the test six times.

Experimental Results

(a) The DDT-resistance of the original and marker strains, their F_1 hybrids and initial analytical populations

The resistance of each of the original wild and marker strains, and the F_1 hybrids between them are shown in Table I. The genotypes of the flies that were selected for testing from the 12 initial analytical populations and their resistance are given in Table II. These results suggest that the dominant gene (or genes) with the strongest resistance is located on the second chromosome of the H-strain. The resistance of the dominant genes on the major autosomes of the K-strain is variable, while the resistance of genes on the second chromosome of the C-strain is lowest. The number and position of the dominant resistant genes and resistance of recessive factors, which a wild strain has in common with the marker strain, could not be ascertained by this experiment. However, it seems certain that the DDT-resistance of adult flies of *D. melanogaster* is a polygenic character and that the original H and K strains were heterogeneous.

(b) Changes of the resistance in analytical populations in the DDT-free environment

The resistance in each analytical population

TABLE II. The percentage of mortality of each initial analytical population

Population		Genotype	Mortality (%)
H_2'	2nd chromosome derived from H	$\frac{sca}{+}$; $\frac{ss^a}{ss^a}$	5.3
H_2''			21.0
K_2'	2nd chromosome derived from K	"	42.3
K_2''			13.3
C_2'	2nd chromosome derived from C	"	50.3
C_2''			52.7
H_3'	3rd chromosome derived from H	$\frac{sca}{sca}$; $\frac{ss^a}{+}$	15.0
H_3''			32.0
K_3'	3rd chromosome derived from K	"	30.7
K_3''			17.3
C_3'	3rd chromosome derived from C	"	40.0
C_3''			44.3

was measured four times during the 720 day cultivation period with the DDT-free culture medium. The results are shown in Table III. A linear regression analysis showed a highly significant decrease in resistance in the H'_2 population and a significant decrease in C''_3. The other lines showed no consistent change. Ample opportunity for crossing-over between the resistant and tester chromosomes was provided. Six of the lines were continued for the full 720 days. It is significant that, while the marker genes were almost completely eliminated, the resistance did not decrease significantly in four of these and in the other two the change was relatively slight considering the long time period.

Each analytical population was cultured for 720 days, and then five pairs of flies were randomly chosen from those populations for analysis and their offspring crossed with each other and with flies of the marker strain. The resistance of these hybrid populations was tested and the results are shown in Table IV. The data from Table IV, after an arc sine transformation, were treated by analysis of variance. The result is shown in Table V.

The hybrid flies represented by $H_2' \times H_3'$, $K_2' \times K_3'$ and $C_2'' \times C_3''$ have the genotype similar to the F_1 hybrids shown in Table I. By this time the originally heterozygous mutant gene had almost disappeared from the population. When the data of both Table I and V were compared, the resistance of the hybrid population, having autosomes derived from the H-strain, slightly decreased and this phenomenon was easily explained by the decreasing resistance of the H'_2 analytical population during long cultivation.

On the contrary, the resistance of hybrid populations, having autosomes derived from the K- and C-strains respectively, did not change appreciably. From the result shown in Table V, no interaction between factors on two autosomes was observed, despite significant main effects of H and K autosomes in all combinations.

(c) The experiment on synthetic populations

Two analytical populations which had been cultured in population cages for 150 days, were mixed together as shown in Figure 11, and introduced into a population bottle. Two sets of such synthetic populations were prepared and one was cultured in the DDT-containing medium and yielded the result shown in Figure 11. The other set was cultured in a DDT-free medium.

In the case of DDT selection, the synthetic population $C'_2 + C'_3$, $C_2'' + C''_3$ derived from the susceptible C and marker strains could not stand moderate DDT selection (DDT-content = 60γ/ml in the medium) and they soon become extinct, but one of them did stand slight DDT selection (DDT-content = 30 γ/ml) for a while.

On the other hand, the synthetic populations composed of K and marker strains or of the resistant H and marker strains, survived both moderate and strong DDT selection. Obviously, the grade of this tolerance was genetically determined. The number of flies in most populations selected by DDT was small, and showed little change for about 40 generations.

After 85 and 120 days' cultivation, two sets of five pairs of flies were taken out of some synthetic populations, and their offspring were examined. The result shown in Table VI indicates that the frequencies of both recessive mutant genes, *sca and ss*^{a} in populations cultured in the DDT-free medium, had decreased, but the *sca* gene on the second chromosome was more severely selected against than the *ss*^{a} gene on the third chromosome in populations cultured in the DDT-containing environment. It may be assumed by this observation that the resistant gene of the marker strain with weaker effect than its allele in the

TABLE III. The changing states of DDT-resistance of the analytical populations

Population	Mortality (%)			
	0	150	360	720 days
H_2'	5.3	12.7	15.7	24.7
H_2''	21.0	*		
K_2'	42.3	40.3	41.0	42.7
K_2''	13.3	33.0	38.0	†
C_2'	50.3	74.3	*	
C_2''	52.7	68.7	55.0	55.7
H_3'	15.0	28.7	18.0	39.3
H_3''	32.0	44.3	44.0	†
K_3'	30.7	62.3	32.0	28.0
K_3''	17.3	39.3	37.3	†
C_3'	40.0	68.3	48.3	†
C_3''	44.3	61.0	71.0	69.7

* Contaminated with wild type flies.
† Untested.

resistant H-strain, was eliminated together with the *sca* gene by the selective effect of DDT. On the other hand, the locus of the resistant gene on the third chromosome seems not to be close to the locus of the ss^a gene.

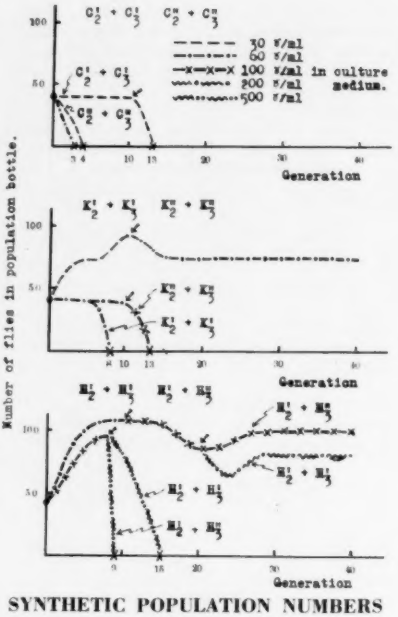
This conjecture was confirmed by another result. The offspring of flies in the synthetic population of $C_2' + C_3'$ cultured in the DDT-containing medium (30γ/ml) were observed. It was found that the susceptible gene on the second chromosome of the C-strain had been more severely selected against than its allele of the marker strain. It may be assumed that the dominant resistant gene is more advantageous in the DDT-containing environment than in the DDT-free environment.

(d) The influence of DDT selection

Two kinds of analytical populations, H_2' and H_3', derived from the H and marker strains cultured for 150 days, were mixed together and the synthetic population was cultured in the medium containing DDT as shown in Figure 11. In the first 10 generations, the DDT-content in the medium was 60 γ/ml, while in the next 10 generations the content was 100 γ/ml and in the last 20 generations, it was 200 γ/ml. After cultivation for 560 days in the DDT-containing environment, the flies from the synthetic population were mated with the marker strain and the F_1 hybrid male flies were backcrossed to female flies of the marker strain.

Then the DDT-resistance of each phenotype among the offspring emerging from the mating was measured. The result was statistically analyzed and is presented in Table VII. The same synthetic population was cultured 170 days more under DDT selection and then the effects of major autosomes and their interaction were analyzed by the following crosses. In this case, another marker strain, having dominant mutant genes, *Pl* (Plum) and *Sb* (Stubble) on the second and third chromosomes respectively, and susceptible C-strain were used. The resistance of a synthetic population, which had a similar genetic constitution in the initial state and was cultured in the DDT-free environment for about 730 days, was simultaneously tested and analyzed.

The new marker strain, which was heterozygous for *Pm*, *Sb* and *Xa* (Xasta), was



SYNTHETIC POPULATION NUMBERS

Figure 11

The chart above shows the change in number of flies in each synthetic population, which were cultured in the environment of existing DDT. An X indicates extermination.

highly susceptible to DDT. The F_1 hybrid male flies having the *Pm* and *Sb* character from crosses between several male flies taken from a synthetic population and several female flies of the marker strain, were mated with the virgin female flies of the Canton-S strain. Then the DDT-resistance of each phenotype among the offspring emerging from the mating was measured. The results were statistically analyzed and are shown in Table VIII. The resistance of a synthetic population, cultured continuously under DDT selection, was thought to be maintained and on the other hand, a non-selected population gradually lost

TABLE IV. The mortality of each analytical group population and their hybrids after cultivation for 720 days

Hybrid		Mortality (%)	Hybrid		Mortality (%)
sca ; ss^a	× H_2'	38.3	H_2'	× H_3'	23.0
"	× K_2'	62.3	K_2'	× K_3'	25.7
"	× C_2''	69.3	C_2''	× C_3''	63.0
"	× H_3'	57.7	H_2'	× C_3''	41.0
"	× K_3'	44.7	K_2'	× C_3''	52.7
"	× C_3''	75.7	C_2''	× H_3'	48.7
sca ; ss^a		80.3	C_2''	× K_3'	43.0

the resistance. From the analytic results, the fall of resistance would be due to the fact that resistant factors on the third chromosome evidently decreased during the long cultivation. The resistant factors on two autosomes of the DDT selected population remained and a slight though significant negative interaction between them was observed, though this might disappear with an appropriate transformation.

Discussion

Tsukamoto and Ogaki[13,14,15] have concluded from their experiment using the same highly resistant H-strain of *D. melanogaster* as in our experiment that a single dominant gene located ca.66 on the second chromosome was responsible for the DDT-resistance. Their analysis was mainly carried out on the larvae; moreover neither the dominant genes on other chromosomes nor any recessive gene was recognized by them. Crow and coworkers[1,2] obtained a highly resistant strain by culturing a large mixed laboratory population in a cage whose inside surfaces were painted with DDT. The most salient points in their experiments were as follows. The DDT-resistance of adult flies in a highly resistant strain was tested by a method similar to ours. They used a marker strain having dominant mutant genes on each major autosome and they could determine not only the effects of dominant factors, but also the effects of recessive factors on each chromosome. From the result of statistical analysis they have concluded that in their strain the DDT-resistance is a polygenic character controlled by one or more recessive factors located on each of the second and third chromosomes and one or more dominant factors on each of the X chromosomes and two major autosomes. The interactions between dominant factors were estimated as responsible for only five percent of the total variance. The chromosomal effects were almost completely additive. The authors have attempted to locate the dominant factors on the second chromosome, but they have only succeeded in finding at least two dominant factors located on the middle part of the chromosome. The difference between the two conclusions of Tsu-

TABLE V. Test for resistance factors after cultivation for 720 days

Pop.	Chr.	Effect	S.S.	D.F.	M.S.	F
H	2	12.69	3863.34	1	3863	33.2**
	3	6.40	984.32	1	984	8.5**
	2 – 3	–2.05	101.27	1	101	0.9
			2326.64	20	116.33	
K	2	6.42	988.17	1	988	7.1*
	3	12.09	3509.00	1	3509	25.1**
	2 – 3	–0.33	2.67	1	3	0.0
			2800.19	20	140.00	
C	2	5.09	622.20	1	622	3.6
	3	1.73	72.11	1	72	0.4
	2 – 3	0.27	1.71	1	2	0.0
			3491.16	20	174.56	
H	2	13.37	4290.70	1	4291	27.3**
C	3	0.10	0.22	1	0.2	0.0
	2 – 3	–1.38	45.38	1	45	0.3
			3139.86	20	156.99	
K	2	7.61	1390.80	1	1391	7.7*
C	3	2.33	130.20	1	130	0.7
	2 – 3	–0.86	17.85	1	18	0.1
			3633.50	20	181.68	
C	2	3.78	342.77	1	343	2.5
H	3	7.41	1318.68	1	1319	9.5**
	2 – 3	–1.05	26.25	1	26	0.2
			2765.99	20	138.30	
C	2	2.70	174.42	1	174	1.4
K	3	10.30	2544.10	1	2544	20.1**
	2 – 3	–2.13	108.80	1	109	0.9
			2533.76	20	126.69	

kamoto and Ogaki on the one hand and Crow *et al.* on the other, concerning the number of resistant genes, is apparently due to the differences in the material and in the measuring method they used. The experiments described in this paper, as well as in Oshima's paper,[11] have disclosed that the effect of the dominant resistant gene on the second chromosome of the highly resistant H-strain was remarkably higher than the effect of the gene on the third chromosome. No resistant gene on the X chromosome could be detected in our experiment, but we have found that the effect of a dominant resistant gene on the third chromosome could not be ruled out. The working hypothesis that the DDT-resistance in *D. melanogaster* is controlled by a complex polygenic system, has been supported by King[6,7] also. Oshima and Hiroyoshi[12] have analyzed DDT and nicotine sulfate resistance in *D. viriliis* and found that dominant genes located on two autosomes were responsible for this property.

From the viewpoint of evolution on the genus *Drosophila*, the fact that there are at least two dominant genes located on two homologous autosomes of these two species, seems to support the preadaptation hypothesis of insecticide resistance and also to give some suggestions on the nature of the polygenic system in this fly. It has been assumed that the genes controlling insecticide resistance have existed at a low frequency in the population, before the insecticide was applied to it. Such a gene may have been somewhat disadvantageous to the population. The culture would become resistant only through selection by the insecticide and regain its susceptibility when it is brought back to the medium without the insecticide.

The same kind of change has been commonly recognized in house-fly populations, although it has seldom been seen in *Drosophila* populations. Crow[2] has found in his resistant strain no perceptible decrease in DDT-resistance after three years' culture in the DDT-free medium. Oshima[11] has reported his observation that his DDT- susceptible populations of the Canton-S strain became resistant

TABLE VI. The number and percentage of each phenotyped fly emerged from the matings which were taken from synthetic populations after cultivation for 85 and 120 days

Pop. \ Phenotype	Cultivation for 85 days +	*sca*	*ss*^{a}	*sca*; *ss*^{a}	Pop. \ Phenotype	Cultivation for 120 days +	*sca*	*ss*^{a}	*sca*; *ss*^{a}
$C_2' + C_3'$	425	103	101	18	$C_2' + C_3'$	336	34	16	2
%	65.7	15.9	15.6	2.8	%	86.6	8.2	4.1	0.5
$C_2'' + C_3''$	369	80	48	18	$C_2'' + C_3''$	509	42	46	8
%	72.5	15.7	9.4	2.4	%	84.2	6.9	7.6	1.3
$H_2' + H_3'$	459	113	65	15	$H_2' + H_3'$	456	60	67	6
%	70.4	17.3	10.0	2.3	%	77.4	10.2	11.4	1.0
$H_2' + H_3''$	356	101	66	12	$H_2' + H_3''$	320	100	37	8
%	65.6	18.9	13.3	2.2	%	68.8	21.5	8.0	1.7
DDT selection. DDT-content : 30 γ/ml in the medium.									
					$C_2' + C_3'$	47	176	0	31
					%	18.5	69.3	0	12.2
$H_2' + H_3'$	266	0	26	0	$H_2' + H_3'$	451	4	37	0
%	91.1	0	8.9	0	%	91.7	0.8	0	0
$H_2' + H_3''$	178	0	15	0	$H_2' + H_3''$	435	0	12	0
%	92.2	0	7.8	0	%	97.3	0	2.7	0
DDT-content : 60 γ/ml in the medium.									
$H_2' + H_3'$	256	0	0	0	$H_2' + H_3'$	567	0	3	0
%	100.0	0	0	0	%	99.5	0	0.5	0
$H_3' + H_3''$	160	0	3	0	$H_3' + H_3''$	391	0	1	0
%	98.2	0	1.8	0	%	99.7	0	0.3	0

after a few generations, when they were contaminated with a small amount of resistant flies and that this resistance was maintained even in a DDT-free environment.

In general, since selection by insecticides should act in combination with natural selection for viability and fertility, resistant factors associated with nearly normal viability would not be selected against. Crow[3] has supposed three possibilities to account for the causes of non-regression in resistance. Among these possibilities, the one assuming that the resistance factors would enter into a new balanced combination with other factors acting as viability modifiers and formerly deleterious factors have become favorable ones, seems to be highly attractive as the explanation of the phenomena stated above. The dominant resistant genes located on two major autosomes which had shown significant interaction, were isolated in the analytical population and were examined to determine whether each of them was selected by natural selection. The result was not clear-cut, but it has been ascertained that the analytical population which had the H-strain second chromosome, on which the strongest resistant gene was located, showed linear regression for a period of long cultivation in a DDT-free medium. In analytical populations, the *sca* gene would be selected by

TABLE VII. Test for dominant resistance factors of the synthetic population cultured for 560 days in the environment of existing DDT

Genotype	$\frac{sca}{+}$; $\frac{ss^a}{+}$	$\frac{sca}{+}$; $\frac{ss^a}{ss^a}$	$\frac{sca}{sca}$; $\frac{ss^a}{+}$	$\frac{sca}{sca}$; $\frac{ss^a}{ss^a}$
Mortality (%)	1.3	19.3	21.7	80.3

	Chromosome	Effect	S.S.	D.F.	M.S.	F
H_2'	2	15.36	5658.01	1	5658	64.9**
H_3'	3	14.87	5307.40	1	5307	60.9**
	2 – 3	—4.51	488.70	1	489	5.6*
			1742.59	20	87.13	

TABLE VIII. Test for dominant resistance factors of the synthetic populations cultured in the environment of existing DDT or no-DDT for 730 days

Synthetic pop.	$H_2' + H_3'$ (DDT selection)	$H_2' + H_3'$ (non-selection)
Mortality (%)	5.0	30.0

DDT selection Genotype	$\frac{+^e}{+}$; $\frac{+^e}{+}$	$\frac{+^e}{+}$; $\frac{Sb}{+^e}$	$\frac{Pm}{+^e}$; $\frac{+^e}{+}$	$\frac{Pm}{+^e}$; $\frac{Sb}{+^e}$
Mortality (%)	5.0	9.7	24.3	64.7

	Chromosome	Effect	S.S.	D.F.	M.S.	F
H_2'	2	14.17	4816.67	1	4817	49.2**
H_3'	3	8.40	1693.44	1	1693	17.3**
	2 – 3	–4.35	464.14	1	454	4.6*
			1956.94	20	97.85	

Non-selection Genotype	$\frac{+^e}{+}$; $\frac{+^e}{+}$	$\frac{+^e}{+}$; $\frac{Sb}{+^e}$	$\frac{Pm}{+^e}$; $\frac{+^e}{+}$	$\frac{Pm}{+^e}$; $\frac{Sb}{+^e}$
Mortality %)	12.3	18.0	59.7	66.7

	Chromosome	Effect	S.S.	D.F.	M.S.	F
H_2'	2	16.21	6305.04	1	6305	32.7 **
H_3'	3	2.81	198.28	1	198	1.0
	2 – 3	–0.008	0.002	1	0	0.0
			3859.93	20	193.0	

$+^e$: chromosome of Canton-S strain.

natural selection and the gene of the marker strain, located near it and responsible for DDT-resistance, would be concurrently selected. The resistance of analytical populations, in which the resistant gene of the H-strain was included, gradually decreased. This phenomenon might be illustrated by the fact that the other resistance factors on the second chromosome were isolated from resistance factors and viability modifiers on other chromosomes. On the other hand, the same presumption could be made on resistance factors on the third chromosome. These phenomena are interesting from the standpoint of co-adaptation between polygenes responsible for resistance.

The observations on synthetic populations cultured in a DDT-containing medium suggest that the resistant genes on two major autosomes were preserved, and if a population had the gene located near *sca* on the second chromosome, it could withstand the DDT effect. The synthetic population showed a decrease of resistance during the long cultivation in the DDT-free environment. In this case, the resistance factors on the third chromosome were markedly increased by selection in the presence of DDT.

As pointed out by Hoskins and Gordon[4] it seems to be important to discriminate between the special factors having detoxifying action on DDT and the general factors manifesting vigor tolerance. This point could not be clarified by our experiment, but the decreasing resistance of populations having heterogeneous resistance genes in the DDT-free environment suggests that some of these genes have such a specific DDT-resisting action. However, for the present, it is difficult to determine whether resistant genes having enzymatic action on DDT-dehydrochlorination exist in *Drosophila*.

The recent data concerning DDT-resistance of the house-fly reported by Maelzer and Kirk,[9] Keiding[5] and Milani[10] have disclosed that a high-level resistance may be manifested by the activity of a single factor on the background of a polygenic system. Lichtwardt[8] has demonstrated that the homozygotes of the R factors have some degree of competitive disadvantage. Thus, there are certain points common to DDT-resistance of the house-fly and that of *Drosophila* which have been disclosed by genetic analyses.

Summary

The resistance to DDT of two wild Japanese strains, as well as that of a laboratory strain of *D. melanogaster*, was analyzed by using a marker strain carrying recessive genes on two major autosomes. The effect of the dominant resistant genes for DDT-resistance located on each of the two autosomes of the adult fly, was analyzed and was attributed to a polygenic system.

The grade of the DDT-resistance was measured by the mortality of the flies exposed to a filter paper soaked with DDT for 24 hours at 75 percent humidity and 25°C temperature. The resistance manifested by the presence of the second chromosome of the resistant Hikone strain was the highest, whereas the effect of the second chromosome of the Canton-S strain was the lowest.

During cultivation in the DDT-free environment of the populations having the resistant gene on each of the two major autosomes separately, the resistance of an analytical population, having the second chromosome of the H-strain, gradually decreased. After cultivation for 720 days, analytical populations were crossed with each other and with the marker strain for statistical analyses of chromosomal effects on two major autosomes. No significant interaction between them was recognized.

DDT-resistance of synthetic populations was clearly determined by their genetic constitution. The resistance of the synthetic population was maintained by DDT selection, but the resistance of a similar population in a DDT-free environment gradually decreased. These phenomena were discussed from the viewpoint of co-adaptation between inter- or intra-chromosome polygenes.

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◆

MALE-STERILITY IN ONION PLANTS FROM TURKEY

Elmo W. Davis*

MALE-STERILITY in the commercial onion has been reported by Jones and Emsweller[3] in the Italian Red variety and by Peterson and Foskett[5] in the variety Scott County Globe. The type of sterility reported by Jones and Emsweller[3] was found by Jones and Clarke[2] to result from an interaction of a recessive nuclear factor and a cytoplasmic factor.

The distribution of the male-sterile gene among several commercial varieties of onions in the United States has been reported by Little, Jones and Clarke.[4] The distribution of the male-sterile gene in onions from various foreign countries has been reported by Davis.[1]

The purpose of this paper is to present evidence on the occurrence of male-sterility in onions from Turkey. The first male-sterile plant was found during the summer of 1954 among three plants of P.I. 204789 grown at Parma, Idaho. (P.I. refers to Federal plant introduction numbers.) In 1956 male-sterile plants were found among seven other introductions from Turkey.

Procedure

Two crosses were made using the male-sterile plant of P.I. 204789 as the female parent: the first was with one of the fertile plants of P.I. 204789 and the second with B 5546 B (Table I). At the same time crosses were made, these two fertile plants were selfed.

In the selfs and crosses grown in 1956 to determine the distribution of the male-sterile gene in onions, a number of the selfed lines segregated for the male-sterile character. These segregating plant introductions from Turkey are shown in Table II. The selfs would be equivalent to an F_2 in which the original parents were not known since the material originally came from open-pollinated stocks.

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Results

The progeny of a testcross of the male-sterile plant of P.I. 204789 to a known B-line — B 5546 B — were all sterile (Table I). A fertile plant of P.I. 204789 used as a pollen parent crossed to the male-sterile plant of P.I. 204789 also gave only male-sterile progeny. It is significant that not only does P.I. 204789 carry the recessive *ms* gene with N-type cytoplasm, but also contains the S-type cytoplasm. Apparently the type of sterility is the same as that reported by Jones and Clarke.[2]

When handling great numbers of bulbs there is always the possibility of being misled by the occurrence of a mechanical mixture. Since many other introductions of *Allium cepa* from Turkey have also segregated for the male-sterile gene (Table II) there is little reason to suppose that the male-sterile plant found in P.I. 204789 was due to chance mixture.

Table II indicates that the male-sterile character occurring in these introductions is recessive and that the results fit a 3:1 ratio. Only P.I. 204789 among these plant introductions has been checked to determine whether the same male-sterile gene is involved as that currently in use in the commercial production of hybrid onion seed.

Conclusion

The gene causing male-sterility in P.I. 204789 appears to be the same as that reported by Jones and Clarke.[2] The S-type cytoplasm as well as the nuclear gene *ms* is present in onions from Turkey.

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TABLE I. Segregation for male-sterility of plants from crosses involving P.I. 204789 onions from Turkey

Pedigree	Genotype	Male-sterile plants	Male-fertile plants
		Number	Number
P.I. 204789 × P.I. 204789	S *ms ms* × N *ms ms*	75	0
P.I. 204789 × B 5546 B	S *ms ms* × N *ms ms*	90	0
P.I. 204789 fertile selfed	N *ms ms*	0	20
B 5546 B selfed	N *ms ms*	0	20

TABLE II. F_2 segregation for male-sterility in onions from eight plant introductions from Turkey

P.I. number	Male-fertile plants	Male-sterile plants	Assumed ratio 3:1 χ^2	P
	Number	Number		
171475	14	1	2.6889	0.10
171478	7	4	.4848	.30
171480	11	5	.3333	.50
172700	7	4	.4848	.30
174020	14	1	2.6889	.10
175571	9	4	.2307	.50
182135	10	5	.5556	.30
204789	2	1	.1111	.70

VARIATIONS IN A POLYDACTYLOUS DESCENT OF MICE

Genotypes and Phenocopies

ROBERT WOHLHUETER*

THE polydactylous strain of mice at the New York State Biological Station at Springville has yielded a number of morphological characters, both genetic and phenocopic. The history of these mice has previously been reported by Strong and Hardy[11] and Engel[3]. All of these variations involved skeletal deformations of the posterior appendages. Four of these new variations were subjected to genetic tests: they were loop-tail, club-foot, pin-tail, and a torsioning or twisting of the digits on the hind limbs.

CONTROL ANIMAL

Figure 12

X-ray photograph of a normal JK mouse, which was used as the control in the present study.

Loop-tail

Loop-tail is a very noticeable shortening and curling of the tail (compare Figure 13*A* and Figure 12). In an *inter se* mating of the F_1 generation none showed loop-tail among 29 mice classified. In the first, second, and third backcross generations to the variant condition a total of 58 mice were classified. Again in this case no loop-tail was observed. This would lead to the conclusion, in itself, that loop-tail is not genetic. However, loop-tail may be phenocopically related to Grüneberg's curly-tail (symbol *ct*) which Grüneberg suggests is caused by a simple recessive gene whose manifestation is greatly influenced by genetic background. A comparison between the two variations reveals that, in loop-tail, the tail is much shorter and the loop more symmetrical than in curly-tail.

Club-foot

Club-foot is another morphological character which occurred in the same polydactylous stock. The character is easily distinguishable from the normal and has little variation. It consists of an abrupt snubbing of the foot, due to a fusion of the foot bones, which renders the foot nearly useless (see Figure 13*B*). This charatcer was observed only in the hind limbs and in no case did it affect both hind legs. The mouse with the original variation died after producing only nine offspring, none of which exhibited the abnormality. The second backcross generation to the variant condition proved similar—eight normals to no club-footed mice.

The above data would lead to the conclusion that this character is also a phenocopy with no detectable genetic background.

Pin-tail

Mice from the same polydactylous stock that produced the above mentioned variations gave rise to another abnormality effecting the posterior regions of the mouse. The variation was termed

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PHENOCOPIC LOOP-TAIL AND CLUBFOOT

Figure 13

A—X-ray photograph of phenocopic loop-tail. Note abrupt ending of vertebrae. *B*—X-ray photograph showing club-foot (left hind leg). Variations proved to be non-genetic.

"pin-tail" because of its characteristic shortening and abrupt tapering ending of the vertebrae of the tail. As illustrated in Figure 14, the tail is shortened to a considerable extent and in all cases easily distinguishable from the normal. However, for convenience and specificity, the mice were broken down into two classifications of the abnormality. The first type, with partially shortened tails (see Figure 14*A-C*) retained the term pin-tail while those with extraordinarily short tails (see Figure 15*A-C*) were assigned the general term brachyury.

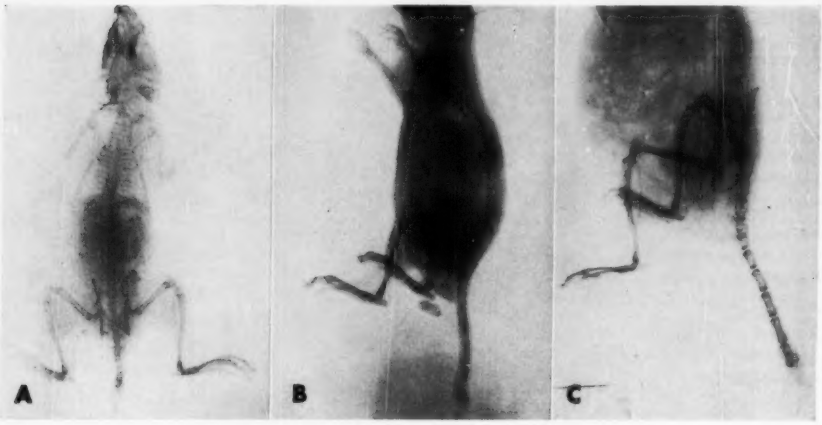
F. H. Clark[2] reported the appearance of brachyury in the descendants of X-irradiated mice. He reported that his mutation was lethal in the homozygous form. Clark suggesetd brachyury to be a phenotypic form of kinky tail, bent-tail, and filiform, all of which are believed to be caused by the same gene. Clark stated that, at that time, the character had not been placed on any of the 14 mouse chromosomes identified at that time.

Grüneberg[7] identified Danforth's short-tail (*Sd*) as being semi-dominant with varying tail lengths. However, he found that in the lethal homozygous state no tail was present. In studying the embryonic development of such mice, he found that the tail developed normally until the 9th or 10th day at which time cellular degeneration set in.

W. F. Hollander and L. C. Strong[8] reported a similar mutation (which they likewise termed pintail) occurring in the 21st inbred generation of the pBr (non agouti, pink eyed, brown) treated with methylcholanthrene. They found the mutation to be definitely dominant and linked to brown. Tail length varied with the shortest belonging to the homozygous group. The trait was definitely distinguishable from normal. Several linkage tests were carried out and a five percent crossover with brown was determined. Hollander and Strong concluded that the mutation was not an allele of brachyury or any other known tail mutation.

Michie[10] has described the combining of the vestigial tail mouse (symbol *vt*—introduced by Heston in 1951) with brachyury. F_1 produced by a cross between the original vestigial mutant stock (*vt/vt, c/c, b/b, a/a*) and the E stock showing brachyury, were backcrossed to a mouse of the original vestigial tail stock. This cross produced 21 mice showing a shortening or absence of the tail as compared to eight normals. He also observed that three of the mice which possessed the tail abnormality also showed an imperforate anus. These mice died within five months after weaning. He has suggested the imperforate anus was the result of the genotype *T/x, vt/vt*.

The present author, however, observed an extraordinarily short pintail (termed



"LONG" PIN-TAIL
Figure 14

A—X-ray photograph of "long" pin-tail. Note seemingly normal upper regions of the tail followed by abrupt ending of vertebrae and irregular tapering of tail. *B*—X-ray photograph of "long" pin-tail. There is evidence that this trait is genetic. *C*—X-ray photograph of "long" pin-tail. Abdominal distortions are the result of pregnancy.

brachyury) in the first backcross generation to a mouse showing the new pintail trait. Similar results soon appeared in other crosses within the pintail stock. In a total of 28 offspring of the first backcross generation nine were observed normal whereas 18 exhibited pintail and one showed brachyury.

A series of sib matings of mice immediately descended from the original mutant produced 17 mice, nine of which were normal, six showed the pintail mutant and one possessed the brachyuric condition.

The author would suggest a dominant gene with possible genetic modifiers is responsible for the trait, with the brachyury occurring as the homozygous genotype. At present, tests are being conducted to establish possible linkage with the JK (short-ear, dilute brown) strain.

Torsion Pollex

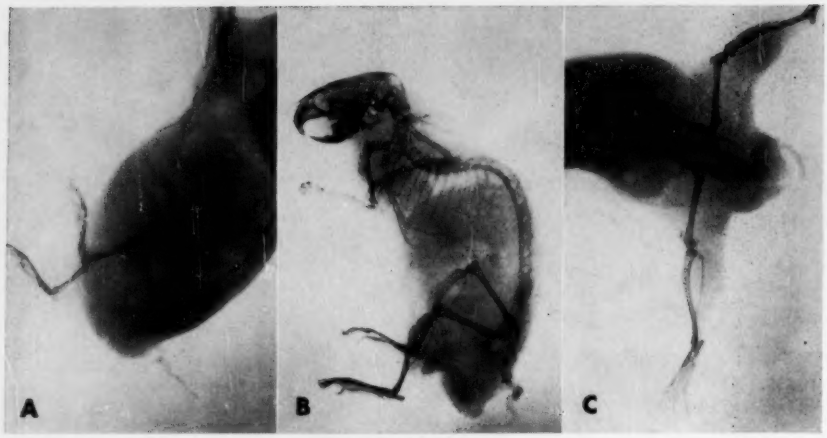
The mice originally acquired by the author from the polydactylous stock at Springville produced offspring which exhibited a new irregularity in addition to polydactylism. This new trait was designated as "torsion pollex" because of its characteristic twisting of the pollex with frequent adjacent digits under the foot (see Figure 16). This torsioned effect was never observed in mice which did not have the polydactylous condition; polydactylism may or may not be accompanied by torsioning.

A series of sib matings of the new torsion mutant resulted in the following: of 141 mice classified 49 were normal, 63 possessed both polydactylism and torsioned pollex, and 29 were polydactylous alone. This means that 92 out of 141 mice exhibited polydactylism; 63 out of 141 showed the torsioning effect and a total of 63 mice had manifestations of torsion out of 92 polydactylous animals.

In the polydactylous mice (those without torsion) the character favored the right foot with 18 occurrences, followed by those exhibiting the character on both hind feet (seven in number) and those with manifestation of left foot only (three in number).

Of the 62 mice in the first backcross generation 28 were normal; 10 exhibited polydactylism alone and 19 expressed torsion and polydactylism.

The variation of expression was simi-



BRACHYURIC MICE
Figure 15

A—X-ray photograph of brachyuric mouse (see text). Note complete absence of vertebrae in elemental tail. *B*—X-ray photograph of brachyuric mouse showing the boneless tail condition. *C*—X-ray photograph of the dorsal view of a brachyuric mouse.

lar to that of the polydactylia character. The right hind foot was favored, followed by bi-lateral expression, followed by manifestation on the left foot alone. But, in the case of those with torsioned polydactylia, double manifestation was most frequent (nine in number) with expresison on the right foot following closely (seven in number) and occurrence on the left considerably less (three in number).

From an F_2 sib mating (poly to torsion poly) the following offspring were obtained: of a total of 58 mice classified, 34 were observed normal; nine showed torsioned polydactylism; and 15 expressed only polydactylism.

From this data the author has concluded that both these morphological characters, pintail and torsioned pollex, are controlled by dominant genes with the trait for polydactylia being epistatic to those for torsion pollex.

Linkage tests of polydactylous individuals and torsioned pollex are now being carried out with JK (short-eared, dilute brown).

Discussion

The preceding data seem to have, at least, two significant bearings upon general biology. First, the discovery of four new variations, some genetic and others phenocopic, add to the sum total of knowledge of the laboratory mouse.

The second significance appears to be more important. In order to ascertain the influence of various agents, such as X-rays, chemicals and atomic radiations, upon the mutation rate of an animal, it first becomes necessary to establish the spontaneous mutation rate in that animal. It follows from the preceding data, that if one includes all new variations that occur in a group of mice as mutations, then the mutation rate thus compiled is invalid. Careful consideration should be given to each variation to determine whether it is truly genetic or simply a phenocopy.

The same precautions might well be applied to the ascertainment of the new mutation rate, since, according to Goldschmidt[4], the very physical influences (i.e., X-ray, chemical, etc.,) which might change the mutation rate, may also effect the rate of producing phenocopies.

Goldschmidt[5] has recently discussed the results of a paper by Landauer[9] and points out that Landauer's conclusions go in the same direction as conclusions he has made from work with *Drosophila*, namely that many sporadically-occurring variations are manifested through phenocopic means. Landauer also asserted that response to agencies inducing a specific phenocopy often varies between stocks of a species.

Therefore one might conclude that, due to sufficient evidence of a high percentage of phenocopies, the validity of mutation rates are dependent upon adequate and accurate tests

TORSION POLLEX
Figure 16

Mouse displaying the torsioned pollex character. Note duplication of first toe (right foot) which is seemingly twisted under the foot.

of the biological variations on which that rate is based.

Conclusions

The present study consists of the description and genetic analysis of four skeletal variations in the house mouse. They occurred in a partially inbred strain of polydactylous mice within a relatively short time. It was shown that two of these are phenocopies of other variations found in other laboratories. Looptail appears to be phenocopically related to curly-tail, whereas club-foot simulates a genetic club-foot described by Bagg and Little[1]. However, in neither case did the variation reappear in a double backcross to the variant condition. Hence, we must conclude that they are not genetic, but phenocopic.

The other two variations, pintail and torsioned pollex, have been shown to be genetic. The relationship of these to known mutations can be determined only by linkage tests. Such tests are being continued. It is concluded that an epistatic relationship exists between polydactylism and torsioned pollex, both of which are governed by dominant genes.

Pintail seems to be the manifestation of a dominant gene influenced by genetic modifiers.

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A PIGEON ENCYCLOPEDIA

DOMESTICATION of the pigeon very possibly antedated that of the chicken and of the horse. Few persons realize the extraordinary evolution which has occurred in this species in the hands of man. The birds we daily see in the city scarcely hint at the diversity existing in the "fancy." For this reason if no other, the information in this book* is a revelation, both in prose and pictures.

The first edition of this work was published in 1941. In August, 1942, the *Journal of Heredity* devoted three pages to a laudatory review by Professor Leon J. Cole of pigeon fame. Sixteen years late this massive book appears in a revised and enlarged edition, handsomely printed and thoroughly up-to-date, even more deserving of praise than before. The author's intent has been to compile and

**The Pigeon.* Wendell M. Levi. (Revised edition.) Levi Publ. Co., Sumter, South Carolina. 1957. xxvii + 667 pp. $20.00.

present in digestible form all available knowledge about domestic pigeons, salted with his own keen comments. For the specialist and for the biologist it is an invaluable source, with a thorough index and a bibliography of over 1,500 references. Of the 12 chapters, the fifth is devoted to Genetics, but the real show is Chapter 2, on breeds and varieties, genetic analyses of which have hardly been touched. The distribution of the book has been worldwide, and there is considerable evidence that genetics is now less of an ivory-tower subject among breeders and fanciers. Such terms as "sex-linked," "homozygous," "heterozygous," and "modifying factors" have even been heard in the show-room! And some fanciers have even taken up experimenting which is analogous to amateurs' in Astronomy. After its long past, what does the future hold for this entertaining as well as useful species?

W. F. HOLLANDER

Iowa State College
Ames

THE MECHANISM OF INHERITANCE OF POLIOMYELITIS

GENTARO GOTO*

RECENTLY, Dr. J. J. Reedy[3] published statistical data on 50 pedigrees of poliomyelitis and concluded that susceptibility is inherited as one autosomal recessive gene with a penetrance of the order of 80 percent. His statistical values, based on a study of the parents and the sibs of propositi, are given in Table I.

From these values the present author calculated the frequencies of the affected and their standard errors. Denote the frequency of affected among parents by P, that among children (sibs of propositi) from matings of normal × normal by X, that among children (sibs of propositi) from normal × affected by Y, that among children (sibs of propositi) from affected × affected by Z, and that among all sibs of propositi by G, then $P = 0.038 \pm 0.012$, $X = 0.090 \pm 0.017$, $Y = 0.250 \pm 0.108$, $Z = 0.333 \pm 0.272$ and $G = 0.101 \pm 0.017$.

A few years ago the present author[1] published some mathematical formulae to analyze the mode of inheritance (dominance or recessiveness), the gene frequency and the manifestation frequency (this has the same meaning as penetrance, but the term "manifestation frequency of a genotype" or "genotypic morbidity" may be better than the term "penetrance of a gene"). When a pathogenetic gene is recessive, the formulae for the frequencies of affected individuals in the groups mentioned above are as follows:

$$P = \alpha q$$

$$X = \frac{\alpha(\tfrac{1}{2}\, p + \beta q)^2}{(p + \beta q)^2}$$

$$Y = \frac{\alpha(\tfrac{1}{2} p + \beta q)}{(p + \beta q)}$$

$$Z = \alpha$$

$$G = \frac{\alpha}{4}(1 + q)^2$$

In these formulae, q is the frequency (or probability of occurrence) of a recessive gene, $p = 1 - q$, α is the manifestation frequency (or the genotypic morbidity) of the homozygous recessives and $\beta = 1 - \alpha$. On the assumption that the pathogenetic gene of the diathesis of poliomyelitis is recessive, the present author analyzed the statistical values of the frequencies of affected by using these formulae and letting $q = 0.075$ and $\alpha = 0.35$, which caused the theoretical values to approach most closely the observed ones. The observed values, the theoretical ones, deviations between them, and the deviations divided by the standard errors are given in Table II.

Each deviation does not exceed the standard

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error of the observed frequency. The greatest deviation is detected for P, where the deviation is equal to the standard error. These show that differences between theoretical values and observed ones are not statistically significant. The frequency of the homozygous recessives in the population is q^2 and the frequency of affected in the population is αq^2. Substituting $q = 0.075$ and $\alpha = 0.35$ in the equations, gives $\alpha q^2 = 0.002$. This is equal to a frequency of two per thousand, which has been observed by Dr. Reedy. In addition, the value of the manifestation rate of 35 percent coincides with that from twin studies by Herndon and Jennings[2].

From the above population genetical analysis, the author concludes that the diathesis of poliomyelitis is inherited by one autosomal recessive gene, the gene frequency is 0.075 and the manifestation rate of the homozygous recessives is 0.35.

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TABLE I. Statistical data on polimyelitis*

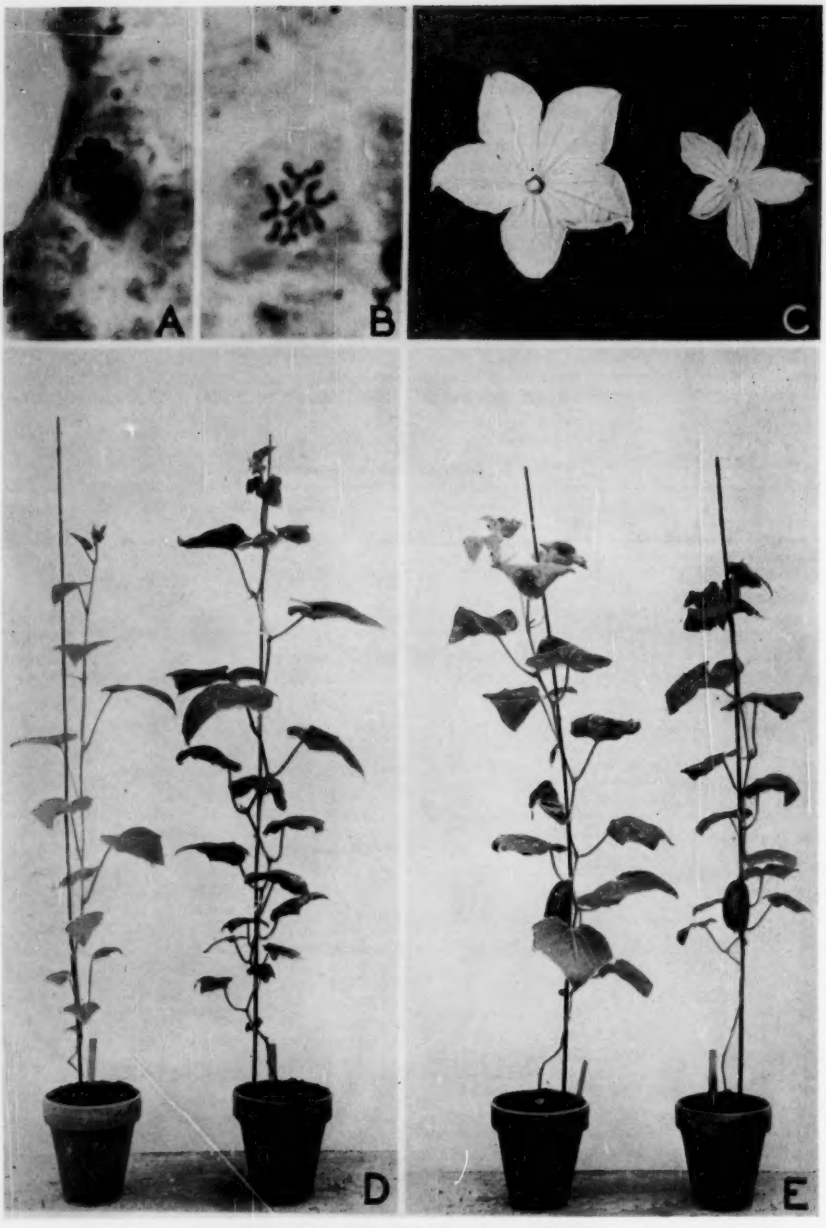
Parents	No. of propositi	No. of all children	No. of all sibs 1)	No. of affected children	No. of affected sibs 2)
Normal × Normal	112	391	279	137	25
Normal × Affected	7	23	16	11	4
Affected × Affected	1	4	3	2	1
Total	120	418	298	150	30

*There are 9 affected among 240 parents. 1) and 2) were calculated by the author, reducing the numbers of propositi from those of all children or of all affected children in accordance with Weinberg's propositus method.

TABLE II. Observed and theoretical values of the frequencies of the affected

	P	X	Y	Z	G
Observed values ±m	0.038 ±0.012	0.090 ±0.017	0.250 ±0.108	0.333 ±0.272	0.101 ±0.017
Theoretical values	0.026	0.096	0.184	0.350	0.101
Deviations |d|*	0.012	0.006	0.066	0.017	0
|d|/ m	1.000	0.353	0.611	0.063	0

*Deviations are given in their absolute values \|d\|; m is the standard error.



MONOPLOID AND DIPLOID CUCUMBERS

Figure 17

A—Metaphase of monoploid plant showing seven chromosomes. *B*—Metaphase of diploid plant showing fourteen chromosomes. *C*—Male flowers of diploid plant (left) and monoploid plant (right). *D*—Monoploid plants. *E*—Diploid plants.

MONOPLOIDY IN CUCUMBERS

LEWIS E. AALDERS*

ALTHOUGH haploid sporophytes have been found in many of the higher plants, there has been no report of haploidy in any species of the family Curcurbitaceae. Haploids usually occur at very low frequencies, and various treatments have been employed in attempts to increase the rate of their occurrence. Although increased frequencies have been reported following interspecific hybridization[5,10], pollination with irradiated pollen [4,6] and delayed pollination[7,11] these treatments have very limited value as general methods of inducing haploidy either because the treatment is successful for only one species or because the increase in frequency is too small to be of any value. In some species, twin seedlings have been found to include a high proportion of haploids especially in certain lines of cotton[9].

By pollinating diploid maize plants with pollen containing a dominant genetic marker, Chase[1,2] was able to select maternal type plants directly from the F_1 progeny. A relatively high proportion of these were haploids. Since the haploids were derived from a basic diploid species, Chase called them monoploids just to emphasize that fact, and the term is similarly used here in reference to cucumbers. Since Chase[3] was successful in producing homozygous diploid maize lines on a practical scale through somatic chromosome doubling in these monoploid plants, a similar study was begun in 1955 with the cultivated cucumber to determine the extent to which monoploid plants would be useful in obtaining homozygous diploid cucumber lines.

Materials and Methods

The genetical method used by Chase[1,2,3] to screen for maternal type plants in progenies of diploids could not be used for cucumbers because no suitable genetic marker was available. On the basis of descriptions of haploids of other species, monoploid cucumber seedlings were expected to be characterized by slower growth, narrower and thinner cotyledons, smaller hypocotyls, and a weaker general appearance than normal diploids. Therefore, the method used to try to identify monoploid cucumber seedlings was to grow large populations of seedlings and make chromosome counts on individuals selected for these characteristics.

In 1955, open pollinated fruits from four unnamed cucumber breeding lines that had been grown by the Plant Breeding Department of Cornell University were used, and in 1956, open pollinated fruits from 41 such Cornell breeding lines were used. Both pickling and slicing type cucumbers were included. Some commercial seeds of the variety Marketer were used in 1955, and in addition, three lines, Cornell 55-615, Ohio M.R. No. 25 and Chinese Long, were self-pollinated in 1956 and used.

The seeds were extracted from each fruit separately. The fruit was cut open, the pulp scraped into a beaker, about 50cc of one normal hydrochloric acid added, and the mixture stirred. The plump seeds soon sank to the bottom of the beaker, and a few immature seeds floated to the top. The floating seeds were embryo-cultured by the method described by Randolph and Randolph[8] for Iris. In 1955, all of the floating seeds were embryo-cultured, while in 1956 only the floating seeds with embryos eight millimeters or less in length were used. All seedlings that were successfully embryo-cultured were checked cyto-

*Dominion Experimental Farm, Kentville, Nova Scotia, Canada. Contribution No. 918 from the Division of Horticulture, Experimental Farms Service, Department of Agriculture, Canada. Based on a thesis submitted to the Graduate School of Cornell University in partial fulfillment of the requirements of the Degree of Doctor of Philosophy. The author wishes to acknowledge his indebtedness to Professor L. F. Randolph, under whose guidance the work was carried out.

logically to determine their chromosome number, usually after they had been transplanted to soil.

The plump seeds were germinated in sand in a greenhouse bench. Heating coils were buried in the sand to maintain a soil temperature of approximately 27° C. The air temperature varied from 18° to 25° C. The seeds were planted two inches by three inches apart at first, but this was soon cut down to one inch by one and one-half inches. When the seedlings were two to three weeks old, plants which appeared to have any of the characteristics expected of monoploids were selected and checked cytologically. The normal plants were discarded.

Chromosome counts were made on squash preparations of very young leaves that were fixed for about 20 minutes in Farmer's fluid and stained for about 20 minutes in hot aceto-carmine.

Results

No monoploid plants were found by making chromosome counts on selected plants that had germinated from plump seeds (Table I). From 34,746 seedlings examined, 374 were selected as being possible monoploids and were checked cytologically (Figures 17*A* and *B*). One was tetraploid, 372 were diploid, and one contained both diploid and tetraploid tissue.

In 1955, four monoploid plants were identified from 21 seedlings that had been embryo-cultured from floating seeds of fully mature fruits (Table II), but no monoploids were found from 222 seedlings that had been embryo-cultured from floating seeds of fruits that were not fully mature.

In 1956, nine monoploid plants were identified from seedlings that had been embryo-cultured from floating seeds. Seven were identified from 194 seedlings from open-pollinated fruits (Table III), and two additional ones were identified from self-pollinated fruits.

Of the four monoploids found in 1955, two were from embryos that were about five mm. long, and the sizes of the other two embryos were not recorded. Of the nine monoploids found in 1956, all were from embryos that were four to six mm. long (Table III). All seedlings obtained from embryos less than four mm. or more than six mm. long were diploid. Normal plump cucumber seeds had embryos that were about 10 mm. long.

When the embryo-cultured seedlings began to grow after having been transplanted to soil, the most vigorous plants in the flats were always diploid. After these were checked cytologically and discarded, the remaining plants appeared to be about equal as far as vigor of growth was concerned. Chromosome counts were necessary to separate the monoploid plants from the diploid plants.

When the monoploid plants had grown to about three inches in height they were treated with colchicine by applying an aqueous solution externally to the region of the growing point. Of the four monoploid plants identified in 1955, two died before colchicine treatment, apparently as a result of infection by some root-rotting organism, and of the nine identified in 1956, one died before colchicine treatment and two died following colchicine treatment. The other eight plants grew to maturity and were similar in vegetative characteristics to diploid plants (Figures 17*D* and *E*). The leaves of the monoploid plants were smaller in area than diploids, but the stems of the two types appeared to be approximately equal in

TABLE I. Chromosome numbers of cucumber seedlings selected as possible monoploids from progenies grown from plump seeds

Seed lot	Seeds planted	Seeds germinated	Seedlings checked cytologically	4*n*	2*n*	*n*
1955:						
Peto Seed Co. H-114 open pollinated	1729	1728	40	0	40	0
Peto Seed Co. H-115 open pollinated	2319	2290	38	0	38	0
Cornell 54-463-5 open pollinated	3511	3430	127	0	127	0
Cornell 54-463-12 open pollinated	3339	3338	41	0	41	0
Marketer (commercial seeds)	4389	4211	61	0.5*	60.5*	0
1956:						
Chinese Long self-pollinated	2050	949	2	0	2	0
Cornell 55-615 self-pollinated	3502	1660	17	0	17	0
Ohio M.R. No. 25 self-pollinated	6306	1511	1	0	1	0
Other open-pollinated lines	20804	15629	47	1	46	0
Total	47949	34746	374	1.5*	372.5*	0

*One plant contained both diploid and tetraploid tissue.

diameter. The monoploid plants grew as rapidly as diploid plants embryo-cultured from similar sized embryos, but diploid plants produced by germinating plump seeds were considerably faster growing than either of the embryo-cultured types.

The lengths of the opened guard cells were measured on leaves of three monoploid and three diploid plants. They averaged 15.67, 15.74 and 15.90 μ for monoploid plants and 21.08, 21.18 and 21.59 μ for diploid plants.

As the monoploid plants grew, they produced very few male flowers but formed female flowers at about the same rate as diploid plants. Usually the monoploid male flowers had very small anthers which did not dehisce (Figure 17*C*), and often when buds of male flowers were produced, they turned yellow and dropped off before reaching one centimeter in length. The diameter of the corolla of monoploid male flowers averaged 25.9 mm., monoploid female flowers averaged 32.9 mm., diploid male flowers 41.7 mm., and diploid female flowers 44.4 mm. The differences between the first three types were highly significant, but the difference between the last two types was statistically insignificant.

Four male flowers were produced by the monoploid plants which apparently arose from colchicine induced diploid sectors. One was produced the first year and three the second year. All had normally dehiscing anthers but when the first three opened, no female flowers opened on the plant that day. The flowers were stored in the refrigerator and used a few days later to self-pollinate the first female flowers that were produced, but in none of the three cases did a fruit result from the pollination. On the day that the fourth diploid male flower opened, two female flowers opened and these were both self-pollinated and both set. The resulting fruits were very similar in appearance to diploid fruits, but when mature, neither contained any visible embryos.

Several other parthenocarpic fruits were produced on the monoploid plants. Four of these resulted from attempts to make self-pollinations by crushing non-dehiscent anthers and smearing the crushed anthers on the stigmas of female flowers. However, no fruits that contained visible embryos were obtained on any of the monoploid plants.

TABLE II. Chromosome numbers of seedlings successfully embryo-cultured from floating seeds, 1955

Seed source	Number of embryos	Number successfully cultured	$2n$	n
Peto Seed Co. H-114 Fruits fully mature	22	3	1	2
Peto Seed Co. H-115 Fruits fully mature	60	18	16	2
Cornell 54-463-5 Fruits not fully mature	591	145	145	0
Cornell 54-463-12 Fruits not fully mature	449	77	77	0

Discussion

The results of the germinating experiments strongly indicate that monoploid embryos are not found in plump cucumber seeds. If they do occur, they are either very rare or they do not germinate. The fact that monoploid plants were obtained only from floating seeds and only from embryos that were four to six millimeters long suggests that most monoploid cucumber embryos are included in this category. If so, monoploid cucumber embryos are probably incapable of germination unless they are embryo-cultured. This is quite different from the situation in maize, for seeds containing monoploid maize embryos are plump and germinate readily[3]. However, the mature maize kernel is composed of the embryo together with a considerable quantity of endosperm, whereas in cucumber seeds there is no noticeable endosperm at maturity. This difference in the amount of endosperm in the mature seeds is no doubt partly responsible for the increased germinating ability.

The reduced size of the monoploid cucumber embryos allows the monoploid embryos to be separated from the majority of the diploid embryos on the basis of whether or not the seeds float. This is an advantage over the genetic marker technique used in maize, because it means that open-pollinated cucumber fruits can be used to produce monoploids. For the genetic marker technique, it is necessary to make controlled crosses before seeds can be

TABLE III. Chromosome numbers of seedlings cultured from various sized embryos of floating seeds, 1956

Embryo length in mm.	1	2	3	4	5	6	7	8	Total
Contaminated	0	0	1	0	12	7	0	0	20
Failed to grow to transplanting stage	1	24	36	33	48	64	12	1	219
Died on being transplanted	0	1	3	9	35	51	19	3	121
Survived and checked cytologically	0	3	4	10	54	83	33	7	194
Diploid	–	3	4	8	53	79	33	7	187
Monoploid	–	0	0	2	1	4	0	0	7

screened for monoploidy.

The attempts to obtain diploid progeny from monoploid plants were not as successful as was expected. Although 13 monoploid plants were found, only eight could be grown to maturity. Four male flowers were produced that had good pollen but the two fruits obtained by self-pollinating with these flowers contained only empty seed coats.

In the early work on maize[3] diploids were obtained from monoploids with a frequency of one diploid line from about 10 monoploid plants. With cucumbers there is the advantage that the plant is indeterminate in its growth habit so it should be possible to carry it along vegetatively and make repeated colchicine treatments until diploid progeny are finally produced. Because of the indeterminate growth of cucumbers and the more exposed growing point, colchicine applications should be more successful in producing diploids from monoploid cucumber plants than in producing diploids from monoploid maize plants.

Summary

Freshly harvested cucumber seeds were separated into two groups on the basis of whether they sank or floated in water upon extraction from the fruit pulp. A total of 34,736 seedlings were grown from plump seeds which sank upon extraction. Of these, 374 were selected as having characteristics expected of monoploid seedlings, but cytological examination proved that none was monoploid.

Embryos extracted from floating seeds were embryo-cultured and of 194 seedlings from selected embryos, seven were monoploid. A total of 13 monoploid cucumber plants were found and are the first haploids to be reported in the family Curcurbitaceae.

All of the monoploids were obtained from floating seeds, 11 growing from embryos that were four to six millimeters long, and two from embryos whose lengths were not recorded. Shorter or longer embryos produced only diploid plants.

Eight of the monoploid plants were grown to maturity and attempts were made to induce diploidy by colchicine treatment, but no diploid progeny were obtained from them.

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CORRIGENDUM

An error has been found in the legend to Figure 11 of my paper, "A Polyhaploid Plant of the Tetraploid Race of *Sisymbrium irio*": *Jour. Hered.* 48:239-242. 1957. The following corrections should be noted: The first line should read: *A* and *C*—Tetraploid; *B*, *D-F*—Polyhalpoid. The last line should read: *D*—6 + 2/2, 6 + 2/2; *E*—6 + 4/2, 4 + 4/2; *F*—6 + 1_{II} + 6.

—T. N. KHOSHOO

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